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MADROÑO

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CLATHRACEAE IN CALIFORNIA

WM. BRIDGE COOKE AND GEORGE NYLAND

Although the Phallales are found mainly in tropical regions there are a few representatives known from temperate areas. Of the two families comprising this order of fungi, the Phallaceae are better represented in the north temperate zone than are the Clathraceae. Nevertheless, many collections have been reported in the United States of some members of the latter family.

The literature on those clathraceous fungi which have been collected in North America is very scattered. In eastern North America, Burt (1894) described *Anthurus borealis* from material collected in New England, and Murrill (1912) added a report, illustrated with a colored plate, of a collection of this species from Blackwell's Island, New York. It is possible that Burt's species and Murrill's record were based on imported material since it has been shown that *Anthurus borealis* Burt is a synonym of *Lysurus sulcatus* (Cooke & Massee) G. H. Cunningham, a species usually found in Australia. *Lysurus texensis* Ellis appeared as a *nomen nudum* in a casual collector's report (Gerard, 1880), and Long (1917) later published a description of another collection from Texas which he provisionally assigned to *L. texensis* Ellis. Lloyd's Synopsis (1909) has not been very useful for North American workers. It is a compilation in which several species are described briefly and illustrated, sometimes poorly; some of these descriptions may prove to represent the same taxon. In "The Genera of Fungi" by Clements and Shear (1931), both *Anthurus* and *Lysurus* are illustrated, the classic illustration of *Lysurus mokusin* credited to Cibot being copied there. Likewise, this illustration is used by Gäumann and Dodge (1928) but credited to "Cibot and Fischer" rather than to "Cibot in Fischer." Coker and Couch (1928) present a description of *Anthurus* and cite the above-mentioned illustrations.

The structure and development of the fruiting body of *Anthurus borealis* were described in considerable detail both by Burt in 1894 and by White in 1944. White referred the material that he studied to *Lysurus sulcatus*. A summary of these two studies was made by Rea and Heidenhain (1955) and a comparison of the characteristics of this species with those of *Lysurus mokusin* was made. This publication, based on the extensive observations made by Rea on specimens from Santa Barbara, California, of *Lysurus mokusin* (Cibot ex Pers.) Fries, represents the first detailed study of material collected in the western part of the United States.

Following his retirement from the directorship of the Santa Barbara Natural History Museum, Paul Marshall Rea devoted much time to

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mycological studies in the Santa Barbara area. His collections and notes are deposited in the Herbarium of the University of Michigan, Ann Arbor, where, through the courtesy of Dr. A. H. Smith, the senior author had the opportunity of studying Dr. Rea's collections of phalloid fungi. Dr. Rea noted the first specimens of *Lysurus mokusin* in Santa Barbara in March, 1941. From that time until the end of his collecting activities he acquired, through his own efforts and those of his neighbors, no less than 130 collections of this species from the Santa Barbara region.

The present paper has grown out of a study of recent collections of clathraceous fungi which appeared in Bermuda grass [*Cynodon dactylon* (L.) Pers.] lawns in Fresno, Yolo, and Sacramento counties, California, particularly after the areas had received an excess of irrigation water. For making available to us the specimens collected in their area, we wish to thank John Bartels, Agricultural Commissioner's Office, Woodland, California, and K. A. Kimble and H. A. McCain, Department of Plant Pathology, University of California at Davis.

The family Clathraceae includes those phalloid fungi (stinkhorns) whose receptacles are stipitate or sessile, clathrate, columnar, or divided into several arms, and whose mucilaginous spore mass is borne on the interior or exterior of the arms or between the arms. In 1931 Cunningham divided the family into three tribes containing eleven genera. The tribe Stellateae, the only one with which we are concerned in California, included the following four genera as keyed out by him:

Arms apically organically united or united by a membrane.
  Glebiferous layer composed of irregular pseudoparenchymatous processes *Mycopharus*
  Glebiferous layer consisting of walls of the chambers of the arms . . *Anthurus*
Arms apically free, connivent or expanded.
  Arms connivent (usually), attached to the apex of a simple cylindrical (or fluted) stem . . . . *Lysurus*
  Arms attached laterally to a horizontal discoid expansion of the apex of the cylindrical stem . . . . *Aseroë*

The other seven genera of Clathraceae were placed in the tribes Columnateae and Clathrateae. In a later treatment, Cunningham (1942) placed *Mycopharus* in synonymy with *Lysurus*; the same organization into tribes was retained. Fischer (1933) recognized fifteen genera in the Clathraceae, but he did not arrange them into tribes. He recognized the four genera listed in the key above, as well as *Pseudocolus*, which Cunningham considered to be a synonym of *Anthurus*.

Mycopharus was established by Petch as a segregate from *Lysurus* in which the glebiferous surface of the receptacular arms is formed of a series of minute shingle-like plates in contrast with that of *Lysurus* in which this surface is merely strongly wrinkled longitudinally, possibly as a result of the compact arrangement of the walls of the stipe chambers in this portion of the receptacle. In 1931 Cunningham accepted this basis for differentiation, but in 1942 he reverted to the earlier position that the two genera were synonymous. In this report Cunningham's 1931 interpretation is being followed and the two genera are considered distinct.

With the exception of some of the Santa Barbara material, which exhibits characters similar in many respects to those of *Mycopharus*, the California specimens studied to date appear to belong in *Lysurus*.

LYSURUS Fr. Syst. Myc. 2: 286. 1822.

Phallus Pers., Syn. Meth. Fung. 245. 1801. *pro min. parte.*

Aseroephallus Lepr. & Mont., Ann. Sci. Nat., Bot. III, 4: 360. 1845.

Anthurus sensu Burt, Mem. Bost. Soc. Nat. Hist. 3: 504. 1894.

Clathraceae; with an egg-like membranous volva; receptacle composed of a glebiferous surface raised on a hollow cylindrical or fluted stipe; stipe white or tinted near the receptacular arms; receptacular arms seated at the top of the stipe, of a more compact tissue, divided into 4–7 arms, arms separate or organically united, grooved on the outside, rounded toward the inside, longitudinally wrinkled, not continuous in the center with the hollow portion of the stipe, covered on the rounded inner glebiferous surface with the ill-smelling gleba.

Type. *Lysurus mokusin* (Cibot ex Pers.) Fr.—only species described in original publication of genus.

KEY TO CALIFORNIA SPECIES OF LYSURUS

Stipe weakly to strongly angular-fluted, upper area red . . . . . *L. mokusin*
Stipe cylindrical, upper area brown . . . . *L. sulcatus*

LYSURUS MOKUSIN (Cibot ex Pers.) Fries, Syst. Myc. 2:286. 1822. Figs. 1, 2. *Phallus mokusin* Cibot, Nov. Comm. Petrop. 19:373–378, t. 5. 1775. *P. mokusin* Cibot ex Pers., Syn. Meth. Fung. 245. 1801. *Mutinus pentagonus* Bailey, Queensland Bot. Bull. 10:35. 1895. *Lysurus beauvaisii* Möll., Rev. Gen. Bot. 12:61. 1900. *Mutinus pentagonus* var. *hardyi* Bailey, Queensland Agr. Jour. 16:494. 1906. *M. hardyi* Bailey, Comp. Cat. Queensland Pl. 747. 1910. *Lysurus sinensis* Lloyd, Myc. Notes 5: 718. 1917.

Peridium white, 3–6 (–11) cm. long, with white rhizomorphs at base; receptacle 6.5–7.5 cm. long to apex of usually connivent arms; stipe 5 cm. long, 4–7 mm. in diameter, narrow at base and expanding upward, white to orange-pink below, dark orange-pink to reddish above, internally divided into hollow chambers, fluted, the flutings 2–3 mm. deep, continuing above into midribs of receptacular arms; receptacular arms 4–6, 1.5–2 cm. long, red, the texture similar to that of stipe, but wrinkled and more compact, the tips of arms pointed; gleba brownish in color, becoming purplish-black when dry; spores hyaline to pale yellowish, rod-shaped, somewhat rounded at ends, (3.8–) 4.5–5 × (1.2–) 1.5–2.0μ.

California collections examined.

In Bermuda grass [*Cynodon dactylon* (L.) Pers.] lawn, Fresno, Fresno County, summer, 1952 (DAV). The stipe in this specimen is hollow, 5 cm. long, 4 mm. in diameter at the base and expanding upward, and pentagonal in cross-section, with the surface flutings 1 cm. from tip to tip of the adjoining pairs. The arms are five in number.

In loam in flowerbed at edge of lawn, Bakersfield, Kern County, April 11 and 22, 1936, *Mrs. A. Ashley* and *Mrs. F. Hamlin* (UC 553876), The collectors thought the fungus might have been introduced from Maine with some cultivated plants. When first picked, the stipe in the later collection was orange above, cream below, and the volva was white; a few days later, the stipe had become entirely orange, the arms red, and the glebal mass madder. The odor was described as that of "acetum squill." Too rapid development because of artificial watering caused cracking and abnormalities. Receptacles with both five and six arms are represented in the collection. In more robust specimens, the receptacular arms may be capped by a portion of the volva. The stipes are made up of at least two, possibly three, layers of chambers.

In lawn, Cajon Street, Redlands, San Bernardino County, May, 1944, *G. J. Hollenberg* (UC 695849). When fresh its color was described as pale pinkish. The specimen is evidently immature; the spores measure $3.8 \times 1.2\mu$, and the stipe (the specimen was collected without the peridium) measures 4 cm. in length and 6 mm. in diameter at the top in the dry condition.

The collection of a specimen in Sacramento late in 1956 is represented only by a colored illustration (fig. 1) made by Norma O'Neil of Sacramento. This illustration, which was sent by the Agricultural Extension Office in Sacramento to the University of California at Davis for determination, clearly represents a sporophore of this species. No herbarium specimen is available.

In garden, Santa Barbara, Santa Barbara County, November 18, 1936, *Miss Caroline Hazard* (UC 568835). Upon the arrival of the specimens at Berkeley, Mrs. Vera M. Miller observed that the stipe was not white anywhere, but pinkish throughout, shading down from a color somewhat lighter than that of the arms to an Ibis pink (Maerz and Paul, 1950, Pl. 1, B–10) where the stipe went into the volva, to a very delicate pink at the lower end of the stipe. The stipe is coarsely chambered above, acuminate below, bearing apically the receptacular arms which were united at their tips. One of the receptacles in the collection bears four arms, while the other has six arms. The glebiferous layer is wrinkled and continuous over the unfused area of the arms and the base of the arms above the stipe. The collector reported that when a hot day was followed by a cool night, the texture of the specimens was crisp, while a cool day followed by a cool night resulted in limp receptacles.

In gardens, Santa Barbara, Santa Barbara County, at least 130 collections made between 1941 and 1952 or later by Dr. P. M. Rea or Mrs. Rea or by residents who gave the specimens to Dr. and Mrs. Rea, the collections all deposited at the Herbarium, University of Michigan, Ann Arbor, and dated as follows: March, 1941; June, 1943; April through Novem-

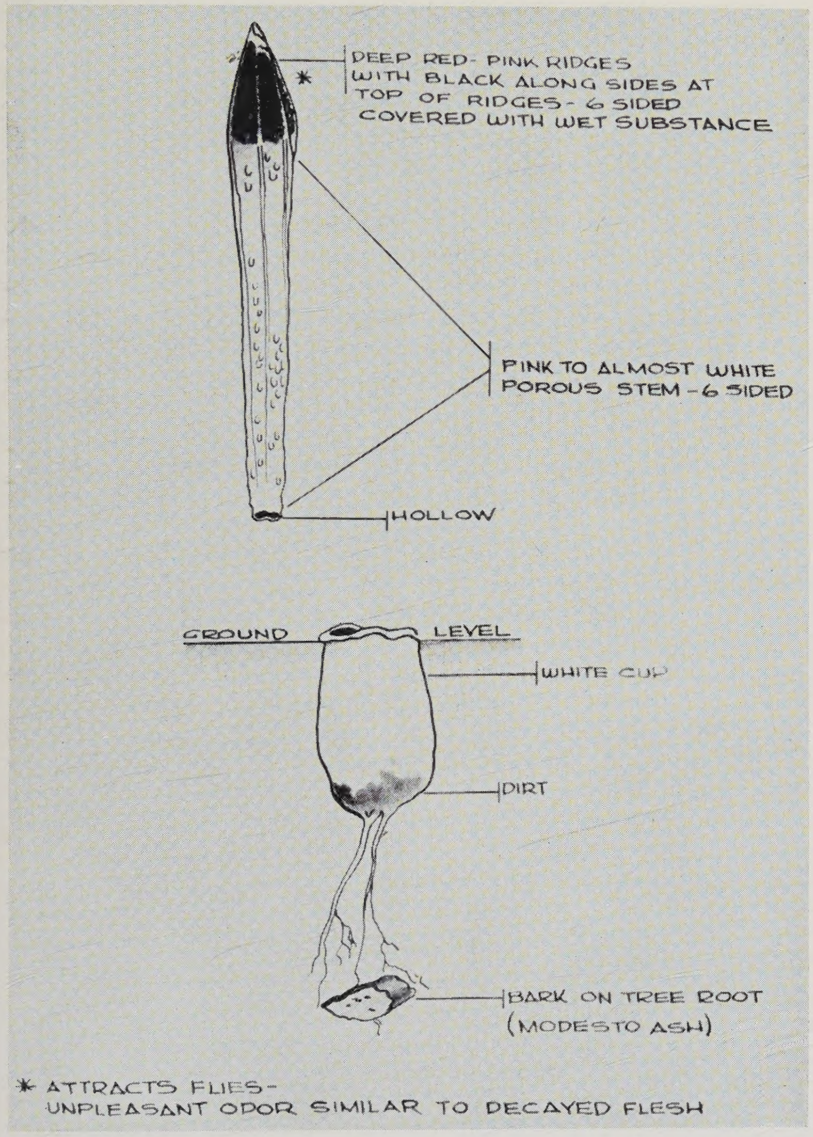

FIG. 1. *Lysurus mokusin* showing habit and mature receptacle. The gleba is shown as occurring between the receptacular arms, not covering their outer surface. Drawing by Norma O'Neil, Sacramento.

ber, 1944; May through September, 1945; May, June, October through December, 1946; January through March, 1947; October, 1952. A wide range of morphological variation is found among these collections as is evidenced in the notes Dr. Rea made from fresh material. On the large mass of earlier material, he took voluminous notes, among which are three different versions of a paper he was preparing on this species. This material was assembled and developed into a paper for publication by Berta Heidenhain (as co-author) at the University of Michigan (1955). The report gives a complete description of *Lysurus mokusin* throughout its development from the very young buttons or eggs to mature and senescent receptacles.

The senior author has made the following general observations from several representative collections of the above series. Dr. Rea sectioned nine peridia and mounted them on black paper. These sections show that in the unopened receptacle the gleba appears to lie on the outer surface of the receptacular arms and not on the inner surface. The gleba is separated, by plates arising from the center of the backs of the arms, into as many units as there are arms. As was pointed out by Rea and Heidenhain (1955), the glebal masses actually lie between the arms and are attached to their sides, but do not invade the central chamber. The backs, or outer surfaces, of the arms are thus free from glebal material. These surfaces are concave or flat in mature receptacles. However, it has been observed by the present authors that as the arms mature and are raised from the volva, the gleba appears to shift in position and surround the receptacular arms on all surfaces except the backs of the arms.

The receptacular arms in the specimens accumulated by Dr. Rea vary from those in specimens in which they are completely free through those which are connivent, those which are held together by fragments or caps of volva material, and those which are organically united by a very small bit of tissue to those which are united in such a way that the receptacular arms form an expanded structure similar to a Chinese lantern and join above the glebiferous surface into an apical spire at least 1.5 cm. long. The longest dry receptacle observed in the Rea collections was 11 cm. long.

Some of the specimens of *Lysurus mokusin* from Santa Barbara, both those of the Reas deposited at the University of Michigan and that of Hazard at the University of California (UC 568835), have characteristics

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Explanation of Figures 2–4.

Figs. 2–4. Development of receptacles in *Lysurus*. Fig. 2. *L. mokusin*. Each of the four fresh specimens shows a different amount of sterile tissue projecting beyond the glebiferous area. Flutings on stipe are apparent and continuous with the outer edge of the receptacular arms between which lies the gleba. Previously unpublished photo by Paul Marshall Rea, Santa Barbara, California. Courtesy of the Herbarium, University of Michigan. Fig. 3. *L. sulcatus*. Cluster of four receptacles in various stages of development. Lower left: young receptacle just breaking through the peridium, the receptacular arms hold the gleba between them; lower right: receptacle with stipe nearly completely elongated, gleba still intact; center: gleba nearly completely removed; upper left: mature receptacle collapsed after removal of gleba. Note cylindrical stipe. Collected at Woodland, and photographed at University of California, Davis, October 1, 1958. Fig 4. *L. sulcatus*. Single receptacle collected at Woodland, September 23, 1958, showing receptacular arms with wrinkled glebiferous surface.

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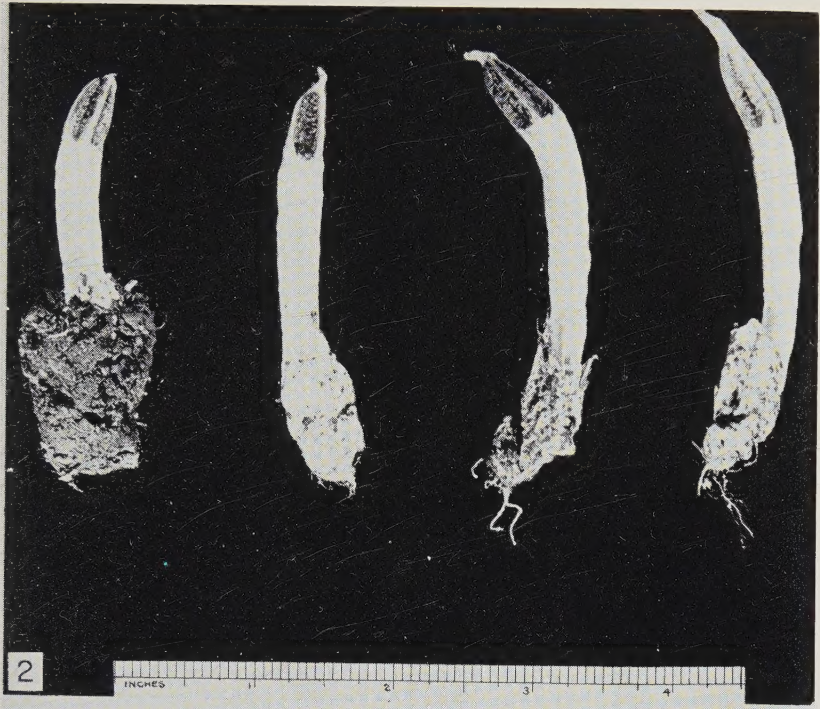

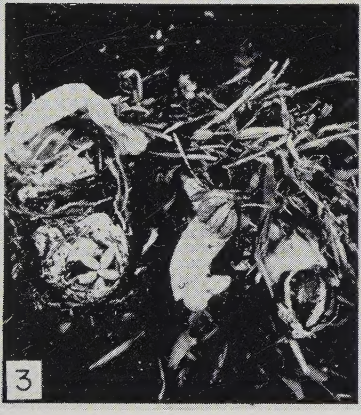

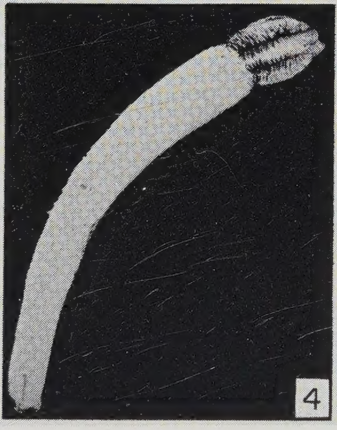

FIGS. 2–4. Development of receptacles in *Lysurus*.

which in many respects are similar to those of *Mycopharus gardneri* (Berk.) Petch of Ceylon. This latter species was first placed in *Lysurus* by Berkeley, then in *Colus* by Fischer. Petch (1919) established for it the new genus *Pharus*, and later, finding the name *Pharus* to be preoccupied, he (1926) renamed the genus *Mycopharus,* distinguishing it from *Lysurus* on the basis of the type of glebiferous surface on the receptacular arms. He illustrated the genus as having the arms slightly separated from one another below the glebiferous surface. Although, as stated above, some of the characteristics of *Mycopharus gardneri,* the type and at first the only species of this genus, are to be found in some of the Santa Barbara collections of *Lysurus mokusin*, the present authors consider that there are sufficient differences between the two species to justify the separation of the two genera. They differ primarily in the nature of the glebiferous surface, which is composed of tightly packed scales of "pseudoparenchymatous processes" in *Mycopharus* and of tightly packed wrinkles in *Lysurus*; in addition, the stipe is weakly fluted in *Mycopharus* and strongly fluted in *Lysurus*. Among the many specimens of *Lysurus mokusin* from the Rea collection of Santa Barbara, however, there is a wide variety of stipe surfaces, the stipes varying from deeply fluted or winged to shallowly or weakly angular.

LYSURUS SULCATUS (Cooke & Massee) G. H. Cunningham, Proc. Linn. Soc. N. S. W. 56 (3):189, pl. viii, figs. 3, 4. 1931. *L. texensis* Ellis in W. R. Gerard, Bull. Torrey Club 7:30. 1880, *nomen nudum. Mutinus sulcatus* Cke. & Mass., Grev. 17:69. 1889. *Lysurus australiensis* Cke. & Mass., Grev. 18:6. 1889. *Anthurus australiensis* (Cke & Mass.) Fisch., Denksch. Schweiz. nat. Gesell. 33:27. 1893. *A. borealis* Burt, Mem. Bost. Soc. Nat. Hist. 3:504. 1894. *Lysurus borealis* (Burt) P. Henn., Hedw. 41:167. 1902. *L. borealis* var. *klitzingii* P. Henn., Hedw. 41:173. 1902. *L. tenuis* Bailey, Comp. Cat. Queensland Pl. 745. 1910. *L. texensis* Ellis (?) in Long, Mycologia 9:271–274. 1917.

Peridium at dehiscence 2–2.3 cm. tall, 2 cm. in diameter at the widest point, rhizomorphic; receptacle 7.5–10.5 cm. long; stipe 6.5–9.0 cm. long, tapering downward, 5–6 mm. in diameter below, 10–13 mm. in diameter at apex just beneath receptacular arms, cream-colored below to yellowish above, composed of one layer of chambers, hollow, apex open, at top of stipe a collar on which are produced 5–7 hollow receptacular arms on the rounded inner surfaces of which is the glebiferous layer; glebiferous layer longitudinally strongly wrinkled, dark olive to blackish; receptacular arms orange-buff to buff to tan in color, composed of very compact tissue with a different appearance from that of stipe, even in length, 6–15 mm. long, 3.5–4 mm. in diameter, tapering to a rather sharp point, more or less flattened on outer grooved surface, the outer surface 1–2 mm. wide, smooth; spores rod-shaped, with rounded ends, slightly yellowish, 3.8–4.3 × 1.5–1.8µ.

In 1880, Gerard noted that Ellis had received a species of *Lysurus* from

Texas which he considered to be new and thus had provisionally named it *L. texensis*. No description was given. In 1917, Long described a *Lysurus* collection from Texas, designating it as *Lysurus texensis* Ellis (?), since this *nomen nudum* had been applied to an undescribed *Lysurus* from Texas. He stated that his material might be only a red form of *Anthurus borealis*. *Lysurus texensis* Ellis in Long is placed in synonymy with *L. sulcatus* because Long's description appears to be based on material of the *L. sulcatus* type rather than of the *L. mokusin* type. In spite of the interpretation by Rea and Heidenhain (1955), Long's description of the stipe is interpreted here as indicating that the walls of the chambers in the stipe wall are polygonal rather than that the stipe itself is polygonal, fluted or winged. Cunningham (1931, 1942) places *L. texensis* in synonymy with *L. sulcatum*, but he lists only Ellis' *nomen nudum* and makes no mention of Long's description.

California collections examined.

In Bermuda grass lawn, Woodland, Yolo County, September 23, 1958, *John Bartels*; October 1, 1958, *K. A. Kimble* (DAV). The specimens usually appeared after occasional heavy spray irrigation. They were either solitary in occurrence, grouped in small clusters, or disposed in large numbers in the lawn. In one specimen, the receptacle, instead of bearing six arms of equal length, bore three arms 1.7 cm. long which alternated with three shorter arms, 1.4–1.5 cm. long.

West Sacramento, Yolo County, October, 1958, *H. A. McCain* (DAV).

In lawn, Fresno, Fresno County, September 16, 1941, *George W. Graves* (UC 660274). Each of the three somewhat immature receptacles bears six arms. The length of the receptacles in the dried condition is 3 cm., while that of the arms is 5 mm.; the stipe is white, with no indication of the original color, had it been other than white when fresh.

Santa Barbara, Santa Barbara County (P. M. Rea collection, University of Michigan, Ann Arbor). Two small specimens are present in this collection.

In flower garden, "The Flower Shop," San Diego, San Diego County, September, 1913, *A. M. Rainford* (specimen in alcohol, deposited by Professor W. A. Setchell in the collection of class demonstration material, Botany Department, University of California, Berkeley). According to Dr. Lee Bonar, who reported the existence of this specimen to the senior author (letter, December 11, 1958, the stipe of this specimen is 6.5 cm. long, 2 cm. in diameter at the apex, and 1 cm. in diameter at the base. There are five receptacular arms, which are free at their tips. Of the five arms, one is shorter than the other four; the short arm is 1.7 cm. in length, while the others are 2.1 cm. in length.

SUMMARY

Even though members of the Clathraceae are not commonly found in California, a large number of specimens of *Lysurus* have been found in a

few isolated localities. The two species of *Lysurus* that have been reported from California, *Lysurus mokusin* and *L. sulcatus*, are distinguished primarily on the basis of color and the nature of the surface of the stipe. Since basidia and spores tend to be similar in appearance and size, gross morphological features such as color, the shape of the stipe in cross-section, the type of glebiferous surface, and the extent of the connection of the apices of the receptacular arms serve as the basis for determining the species in the genus *Lysurus*. On the whole, these characters seem to the writers to be of importance only at the species level at our present stage of knowledge of the Phallales. However, the nature of the glebiferous surface of the receptacular arms is considered to be of sufficient importance to separate the two genera, *Lysurus* and *Mycopharus*.

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FOLIAR XEROMORPHY OF CERTAIN GEOPHYTIC MONOCOTYLEDONS[1]

BAKI KASAPLIGIL

INTRODUCTION

Xeromorphy in the vegetative organs of plants and especially in foliage leaves has long attracted the interest of morphologists and ecologists. There is now considerable information about foliar xeromorphy and its relation to factors of the environment (Clements 1905, Harshberger 1908, Starr 1912, Hanson 1917, Hayden 1919, Pool 1923, Mothes 1932, Evenari 1938, Shields 1951a). Most of these studies deal mainly with dicotyledons, while the monocotyledons, with the exception of xeric grasses, have received less attention. As a matter of fact, dicotyledons are more abundant than monocotyledons in arid and semi-arid regions; however, certain "drought resistant" monocotyledons do occur widely in xeric habitats.

Geophytic monocotyledons, i.e., those having subterranean bulbs, corms, rhizomes, or tuberous roots, are quite common in the steppic flora of central Anatolia. In the vicinity of Ankara, there are over fifty such species in the Gramineae, Araceae, Liliaceae, Iridaceae, and Orchidaceae; they form about thirty-seven per cent of the total number of known species of monocotyledons in the local flora (cf. Krause 1937). In the present study the foliar xeromorphy of eighteen of these species, representing five families, has been investigated anatomically.

The geophytic monocotyledons in central Anatolia produce aerial shoots as early as February and complete their flowering and fruiting stages during March and April. After forming seeds they usually return to subterranean dormant stages before the drought period starts. In their habit of resting during the dry season, they resemble ephemeral annuals. Some botanists may not consider the ephemerals and geophytes as true xerophytes, since both of these groups escape instead of endure the critical drought period. This argument may be answered by considering the dormant seeds or subterranean fleshy organs as adaptational drought-enduring stages in the continuous life cycles of these plants. The geophytes thus fit the "drought evading" class of Shanz (1927). Furthermore, the geophytes can also be considered as succulent xerophytes since they are well adapted to withstand prolonged drought by means of their fleshy subterranean organs in which water, carbohydrates, and mucilaginous substances are stored (cf. Warming 1909).

In this paper, the term "xerophyte" is used as a convenient qualitative term to designate the plants of xeric habitats where the available soil water is limited. The classical concept of this term refers to plants living in places with limited water supply and which are equipped with various arrangements to reduce transpiration (cf. Willis 1957, p. 692). Although

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[1] This paper was supported in part by a faculty research grant from Mills College.

Bakee (1914) concluded that xerophytes have higher indices of transpiring power than mesophytes, recent experimental studies have demonstrated that there is no direct correlation between structural modifications and transpiring powers of xerophytes. The degree of drought resistance cannot be judged simply according to the xeromorphic features (Maximov 1931, Evenari 1938, Weaver and Clements 1938, Shields 1950, Daubenmire 1959).

There is general agreement that xerophytes can by morphological and physiological means either escape or resist permanent injuries caused by excessive loss of water (Maximov and Maximov 1924), and leaf xeromorphy is, in addition to geophytic xeromorphy, another such means. Studies on leaf xeromorphy and its relation to physiological and structural influences are discussed comprehensively in a recent review article by Shields (1950); therefore the present paper will not attempt to give a detailed account of the environmental and genetic causes of the foliar xeromorphy. However, I should like to point out briefly the factors of the steppic environment in central Anatolia that contribute to the structural modifications of xeromorphic leaves in the eighteen geophytic monocotyledons chosen for investigation. In Ankara the atmosphere is very dry and induces strong transpiration. The wind velocity is high during the winter months when foliage leaves of many geophytic monocotyledons develop. The wind increases the rate of transpiration. The light intensity, one of the factors contributing to foliar xeromorphy (Shirley 1929, Turrell 1940, Shields 1951a) is very strong due to high altitude (from 830 m. at the railroad station to 1855 m. on the Elmadag mountain), cloudless skies, with the exception of a few rainy and snowy days distributed irregularly through fall and winter, and to the reflection of solar radiation from gray steppic soils and calcareous rocks of the mountains which are poorly covered by vegetation. The precipitation is low, and the drought period usually extends from May to October (Colasan 1946, Walter 1955 a and b). The limited water supply of the steppic soils is further decreased by direct evaporation from the soil surface, and the soil solution acquires the high osmotic pressure which is so typical of arid and semi-arid regions. Also, the steppic soils in this habitat are extremely deficient in nitrates, which is another important factor contributing to foliar xeromorphy (cf. Mothes 1932).

The monocotyledons in this study exhibit certain uniformities in addition to their geophytism, reduced leaf surface, and phenological periodicity. Their root systems are fibrous and very shallow and are limited to the uppermost soil layers (Birand 1938, Karamanoglu 1955). The latter author points out the anatomic similarities in regard to epidermis, exodermis, cortical parenchyma and endodermis in the roots of *Iris*, *Ornithogalum* and *Muscari* species, although these tissues show minor differences from one species to another in regard to thickness of tissues. Furthermore the geophytic monocotyledons studied by Birand (1938) exhibit low osmotic pressures since they complete their activities above ground during the moist season. The present study was initiated primarily to see if there is any parallelism in the structural modifications and in the adaptational degree of foliar tissues among unrelated species of geophytic monocotyledons.

In this study the following widely accepted xeromorphic characters have been considered:

A. General habit of the plant and gross morphology of leaves
  1. Reduction of the surface
  2. Revolute margins
  3. Folding and fusion of the blade
  4. Involution upon wilting
  5. Increased thickness of the blade
B. Epidermis
  6. Strong cutinization
  7. Increased thickness of the epidermal cell walls
  8. Water storage in depression of stomata
  9. Cutinization and ledge formation on the guard cells
  10. The occurrence of trichomes
  11. Water storage in the epidermal cells
C. Mesophyll
  12. Isolateral organization of the palisade
  13. Strongly developed palisade parenchyma at the expense of spongy parenchyma
  14. Compactness of the tissues
  15. Decreased size of cells
  16. Development of a water storing tissue
  17. Abundance of excretory idioblastic cells
D. Vascular system
  18. Strong development of vascular bundles
  19. Compactness of vascular bundles, i.e., lateral proximity of veins
E. Sclerenchyma
  20. Strongly developed fibers, tracheoid and sclerenchymatous idioblasts (cf. Foster 1956 for these idioblasts).

MATERIALS AND METHODS

The leaves were collected from plants growing in different localities of the steppe of Ankara. Portions of leaves were fixed in a solution of formaldehyde–propionic acid–acetic acid, then transferred into 70 per cent ethyl alcohol. Transverse leaf sections were made by free hand and stained with safranin for general histological study and mounted in gelatin-glycerin. Additional sections were stained with phloroglucinol and hydrochloric acid for lignin test. Sudan IV was used for the cuticle (Foster 1949). Leaf portions, cleared in 3 per cent sodium hydroxide, stained with safranin, dehydrated with xylene and mounted permanently in Canada balsam (cf. Kasapligil 1951 for method), were entirely satisfactory to observe the orientation of various tissues and their cellular morphology. Drawings of leaf sections were prepared by camera lucida. Herbarium specimens of the plants were also prepared and distributed among the herbaria of the University of Ankara, University of California, Berkeley, and the Royal Botanic Garden, Edinburgh.

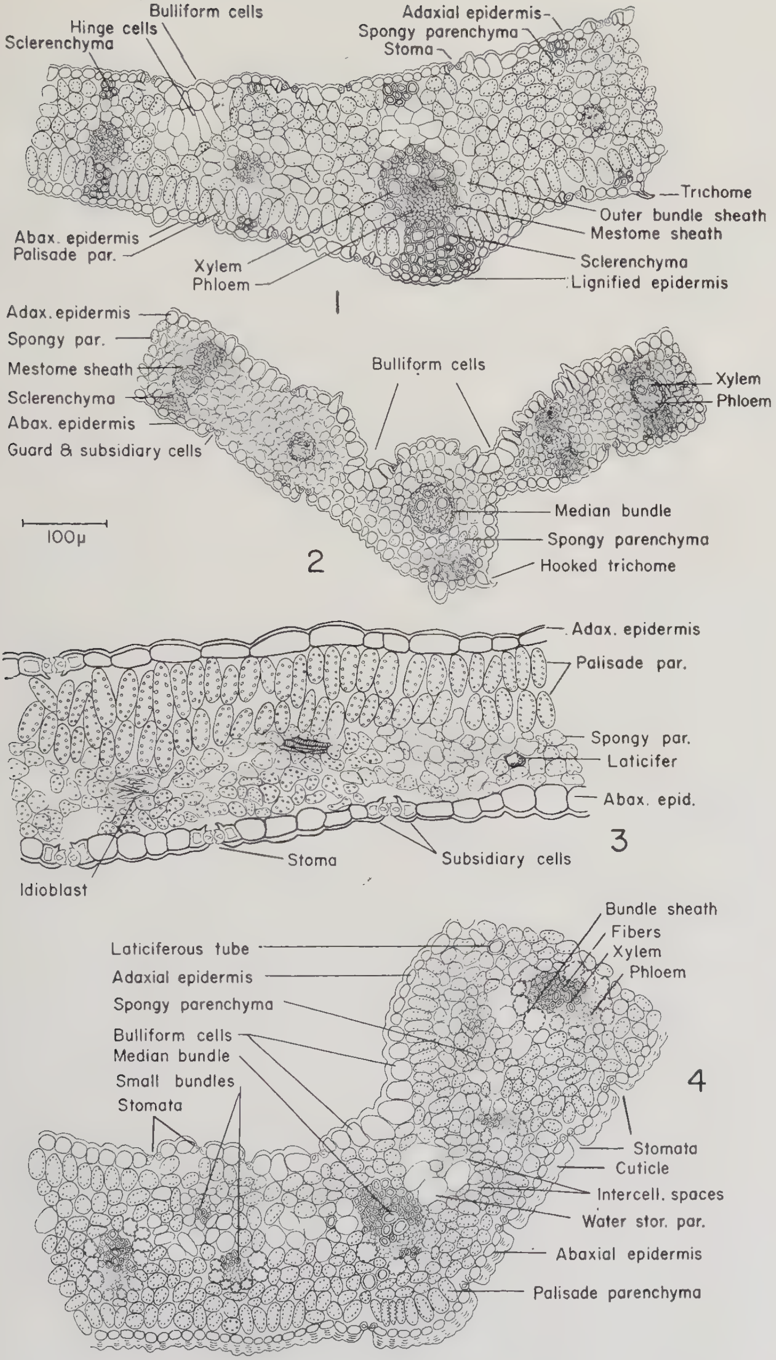
DESCRIPTIONS OF PLANTS AND THEIR COMPARATIVE FOLIAR ANATOMY

GRAMINEAE

HORDEUM BULBOSUM L. (fig. 1) is a tall perennial grass of cultivated lands as well as of the mountains of the steppe. The flat stiff blades are characteristically involute upon wilting. The blades are 6–10 mm. wide, 230–300 microns thick along the median bundle and 150–160 microns thick in the lateral portions. The cormous basal nodes are aggregated in large clumps.

Epidermal cells are elongated with undulate cell walls, and alternate with short silica cells. Outer cell walls of the epidermal cells are thicker than their inner tangential walls. Cutinization of the cell walls is not prominent, but the epidermal cells adjacent to sclerenchyma strands on both adaxial and abaxial surfaces of the blade have lignified cell walls. The stomata are not sunken, and they occur on both surfaces. The guard cells are dumb-bell shaped and have lignified cell walls. Each stoma is accompanied by a pair of subsidiary cells. Bulliform cells are situated along the grooves of the adaxial surface in 4–6 rows. They have straight cell walls. Hinge cells underlying the bulliform cells are filled with water, contain very few chloroplasts and form one or two layers. Two different types of unicellular trichomes were observed: short and hooked trichomes with thick silicified walls along ridges on the abaxial surface and along margins of the blade; long slender trichomes with lignified cell walls near the abaxial base of the blades.

Leaves are dorsiventral and a single layer of palisade parenchyma is situated on the abaxial side. Cells of the mesophyll are small and very compactly arranged. Prismatic crystals are abundant in the spongy parenchyma cells along the bundles. Collateral bundles are surrounded by mestome sheath (Schwendener 1890) as well as by bundle sheath. Bundle sheath extensions (Esau 1953) are well developed, especially along the median bundle of the blade, and connect the vascular bundles to the adaxial fibre strands as seen in transverse sections. Vascular bundles are close together and are interconnected by small bundles. Fibres are more strongly developed on the abaxial sides of the bundles than on the adaxial ones. Abaxial fibre strands are connected directly with the lignified epidermis and the mestome sheath of the bundles, while the adaxial fibre strands are "separated" from the bundles either by bundle sheath extensions along large bundles or by spongy parenchyma cells along small bundles. Strands of 8–15 fibres extend along both margins of the blade, beneath the epidermis.



FIGS. 1–4. Transverse sections of leaves: 1, *Hordeum bulbosum*; 2, *Poa bulbosa*; 3, *Arum orientale* var. *elongatum*; 4, *Allium rotundum*.

Poa bulbosa L. (fig. 2) is a small perennial grass which is very common in the steppe as well as in the fields and fallow lands. It has short and narrow leaves, involute upon wilting. The blades are 2–4 mm. wide and 4–7 cm. long. Thickness of the blades ranges from 180–220 microns along median bundles and from 60–125 microns in the lateral portions. The basal portions of the shoots are swollen and enveloped by thickened bases of leaves forming clumps of small bulbs.

Epidermal cells are long tabular cells with straight walls. Outer walls are thicker than the inner ones and are moderately cutinized. The bulliform cells are 5–6 cells wide, situated along two grooves of the adaxial surface on two sides of the median bundle. Bulliform cells are not accompanied by hinge cells. The stomata are slightly sunken and occur in both surfaces of the blade above assimilatory tissue. Guard cells are dumbbell shaped, and each stoma has two very small subsidiary cells which are also sunken. Unicellular hooked trichomes are situated along both margins and dorsal ridges of the blade.

Mesophyll is not differentiated into palisade and spongy parenchyma. It consists of very small isodiametric parenchyma cells closely packed together. Mesophyll is only two cell layers thick beneath the bulliform cells, while its thickness in other portions of the blade is 5–6 cell layers. Prismatic crystals are abundant throughout the mesophyll parenchyma.

The collateral vascular bundles are surrounded by mestome sheaths, but differentiated border parenchyma or bundle sheath extensions are not present. The median bundle is "imbedded" directly within assimilatory tissue and is not connected with the dorsal strand of fibres. On the other hand, most of the small bundles are connected to upper and lower epidermis by strongly developed fibre strands. Groups of 3–6 fibres extend along leaf margins beneath the epidermis. Comparatively speaking, the vascular bundles in the *Poa* leaf are more compactly arranged than the vascular bundles of the *Hordeum* leaf, and likewise anastomosing veins are more frequent than those in the previous species.

ARACEAE

As far as this author knows, this family is represented only by one species in the steppic flora.

Arum orientale M. Bieb. var. elongatum Engl. (fig. 3) is a herbaceous perennial plant which grows in little soil pockets on eroded and exposed limestone or within narrow rock crevices at the highest altitudes of the steppic region. Broadly-hastate leaves are 15–25 cm. long. The lamina is tender and 250–270 microns thick. The adaxial surface of the lamina is darker green than the abaxial one. The plants have rounded tubers, slightly adpressed.

The epidermal cells are polygonal and appear isodiametric in face view. They are about 50–70 microns long and 40–50 microns deep in transectional view. The epidermal cells along the vascular bundles are narrow tabular in form. A few chloroplasts were observed within the epidermal cells. Outer tangential walls of the epidermal cells are cutinized moderately and these walls are thicker than the inner tangential and radial ones. Stomata are not sunken and appear on both surfaces of the lamina, more frequently on the dorsal side. As an average, the guard cells are 45 microns long and 15 microns wide, although their sizes are variable. The inner and outer ledges of the guard cells are distinctly developed. Each stoma is subtended by a pair of lateral subsidiary cells which are thick walled. Each subsidiary cell is equipped with a curved ledge on its inner tangential wall adjacent to the guard cell. Possibly these ledges produce complete closure of stomatal openings and form an additional air chamber between the guard cells and the substomatal air cavity. Trichomes and idioblasts are absent in the epidermal tissue.

Mesophyll is dorsiventral and provided with a biseriate palisade parenchyma on the adaxial side. Palisade parenchyma cells are large and occupy the upper half of the mesophyll. The spongy parenchyma consists of 5–6 layers of large irregular and loosely arranged cells. As a whole the mesophyll has very conspicuous intercellular spaces presenting a mesomorphic rather than a xeromorphic structure. Idioblasts containing raphides are distributed within the spongy parenchyma. Individual raphides are 180–200 microns long and form crowded bundles within the idioblasts. Druses are also present, but are not as common as raphides. Another feature of the spongy mesophyll is the presence of articulated laticifers which were noted also by Solereder and Meyer (1928). Sclerenchyma is not present in any form.

Vascular bundles are reticulate and the leaf resembles a dicotyledonous leaf in this respect. The veins of first, second, third, and fourth orders are closed and form vein islets, while the veins of fifth and sixth orders frequently end freely in mesophyll. Marginal bundles run very close to the leaf edge. The major veins are surrounded by a vaguely differentiated bundle sheath.

Liliaceae

This family is represented by eight genera in the steppic flora. The largest genus, *Allium*, is represented by ten species occurring in the steppic region under a wide variety of conditions, from moist places along streams to extreme xeric habitats of saline depressions and mountain steppe. Two species, which seem to endure drought longer than other species, were studied.

Allium rotundum L. (fig. 4) is a tall slender plant reaching a height of 40–50 cm. The leaves are filiform, tapering gradually to the tips. Although the leaves are typically unifacial in their ontogeny, the adaxial surface is flat, the abaxial one ridged (cf. Esau 1953 and Hayward 1938 for the ontogeny of the leaf of *Allium cepa*). There is no central cavity in the blade. Upon wilting, involution takes place through a folding action along the median bundle of the lamina halves. The leaves are 2 3 mm.

wide and 280–300 microns thick. The thickness decreases very slightly toward the margin of the blade. The small bulbs are oval in outline.

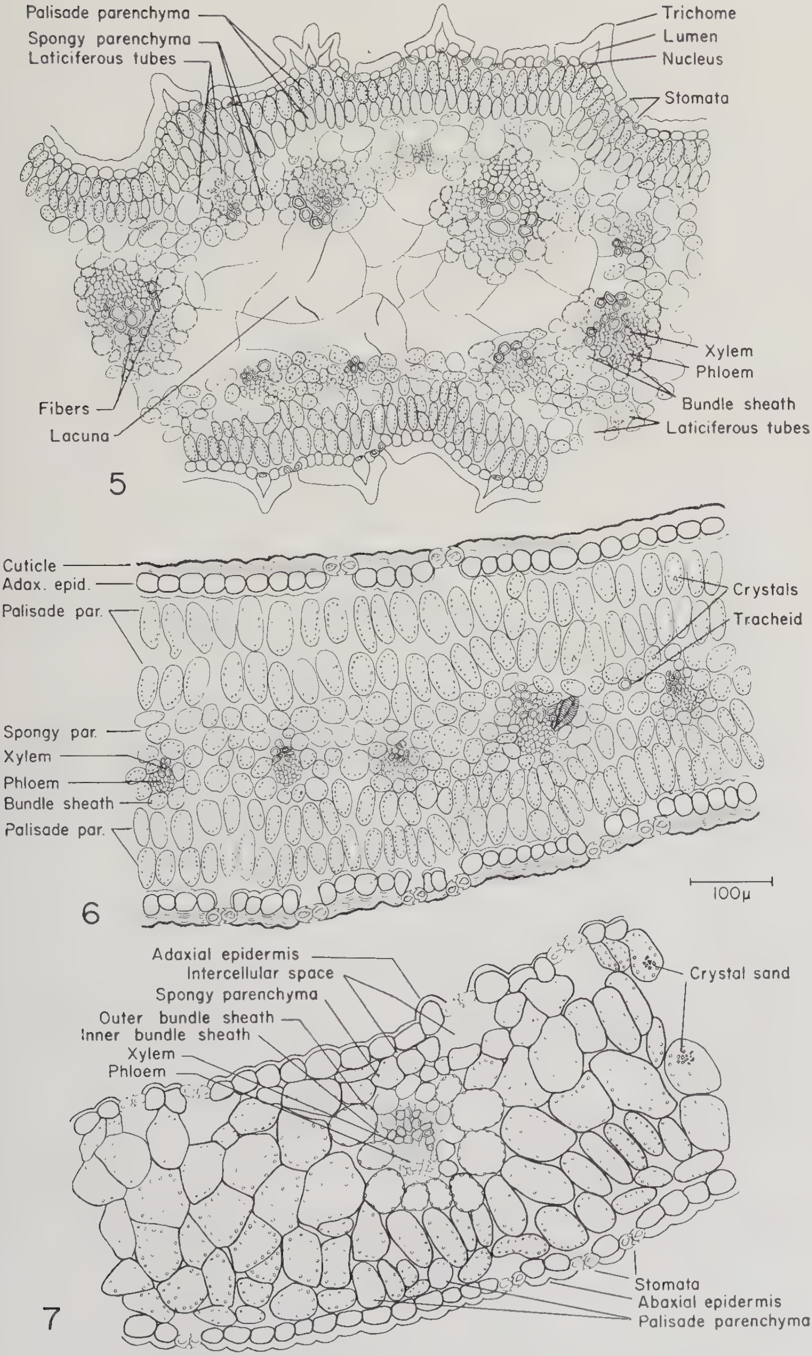
The epidermis, as seen from the surface, consists of long, tapering cells with straight lateral walls. The lower epidermis bears a much heavier cuticle than the upper and its outer walls are characterized by lamellation. The lumina of the lower epidermal cells are extremely small. Bulliform cells of the upper epidermis extend along the groove above the median bundle and form a row of 5–7 cells. They are not accompanied by any specialized hinge cells in the underlying tissue. Stomata occur on both upper and lower surfaces and are sunken below the epidermal level. Subsidiary cells are not present, and trichomes in the epidermis are missing.

Mesophyll includes a uniseriate palisade on both sides. The abaxial palisade is strongly differentiated, while the adaxial one is weakly developed. The spongy mesophyll is composed of small isodiametric parenchyma cells which form 10–15 layers with conspicuous intercellular spaces. A well differentiated water-storing parenchyma in the central portion of the mesophyll consists of enlarged cells lacking chloroplasts. Articulated laticifers and patches of tracheoid idioblasts are abundant in the mesophyll and are distributed at random. Well developed vascular bundles are densely arranged in longitudinal directions. They are transconnected by means of small bundles. Reversal of the bundles in regard to the position of xylem and phloem is obvious. Apparently this situation is caused by the peculiarity of the leaf apex (cf. Esau 1953, fig. 16.19). Clearly differentiated bundle sheaths have cells characterized by prominent central vacuoles and peripherally arranged chloroplasts.

Fibers associated with the vascular bundles are strongly developed, the xylem fibers, especially, forming very thick and compact strands along major veins.

ALLIUM STAMINEUM Boiss. (fig. 5) is a small plant about 20–25 cm. high with tunicated oval bulbs. The leaves are smaller and more tender than those of the previous species. They are 1.5–2 mm. wide and appear reniform in transverse section. Involution upon wilting is not pronounced. The thickness of the leaves ranges from 450 to 550 microns. As in *Allium rotundum*, the leaves are unifacial, but both the upper and lower surfaces are ridged. The epidermal cells are tabular in form, and their outer walls are extremely thick and heavily cutinized throughout both surfaces of the leaves. Consequently the lumina of the epidermal cells are very small. Stomata occur in deep depressions of abaxial and adaxial surfaces. Unicellular, short, conical trichomes with very thick cell walls are arranged in regular rows along the ridges. Trichomes are living cells, and their nuclei are always situated at the bottom of the enlarged basal portions of the cells.

The mesophyll is quite different from that of *A. rotundum*. First of all it has a well developed biseriate palisade on both upper and lower sides,



FIGS. 5–7. Transverse sections of leaves: 5, *Allium stamineum*; 6, *Colchicum biebersteinii*; 7, *Gagea arvensis* var. *semiglabra*.

followed by a layer of articulated laticiferous tubes. These laticifers possess perforation plates similar to sieve plates. The spongy parenchyma is very weakly developed, forming a layer of 2–3 cells inside the "ring" of laticifers. As the leaves reach maturity, remarkably large water-storing parenchyma cells in the center of the leaf collapse and form lacunae. Collateral bundles are surrounded by bundle sheaths. "Parallel" running major bundles are more or less spaced from each other, but they are transconnected by minor bundles. There are a few xylem fibers associated with the bundles, but phloem fibers are very rare. Sclerenchymatous idioblasts are abundant and seem always to be associated with interconnecting transverse bundles or to occur terminal to freely ending veinlets.

COLCHICUM BIEBERSTEINII Rouy (fig. 6) is a stout plant which grows in foothills and on mountain slopes protected from the wind. It blooms as early as in February, right after a few sunny winter days. The basal leaves arising from tunicated bulbs lie on the ground. They are flat, narrow, dark green and coriaceous in texture, 8–10 mm. wide and 380–450 microns thick. Involution does occur, although the leaves are not provided with any specialized motor cells. A similar situation was observed in *Oryzopsis hymenoides* (Roem. et Schult.) Ricker by Shields (1951b). The epidermal cells are long tabular cells with straight anticlinal walls. Abaxial and adaxial sides of the epidermis are coated with a thick cuticle layer which exhibits very fine dentation as seen in transectional view. Outer tangential walls of the upper and lower epidermis are exceedingly thick and are marked with distinct lamellation (25 microns or even thicker) while the inner tangential walls are moderately thickened. Radial walls of the epidermal cells however do not show a noticeable thickening. The stomata occur on both surfaces, but are more frequent on the abaxial surface. They are not sunken, but lie at the same level with cuticle and thick outer walls of the epidermal cells. The guard cells also possess very thick cell walls and are provided with well developed inner and outer ledges. Subsidiary cells are not present. Unicellular, short, conical trichomes with blunt tips occur along leaf margins only. These trichomes are dead cells with extremely thick walls and practically no lumens.

The leaves of *Colchicum biebersteinii* present an isolateral organization with a biseriate palisade on both upper and lower sides of the mesophyll. Palisade parenchyma is strongly developed at the expense of the spongy parenchyma. It occupies two thirds of the mesophyll. Palisade parenchyma has thin walls in general, but the outer cell walls of the outer parenchyma layer are remarkably thickened toward the leaf margins. The spongy parenchyma is scanty and represented by 2–5 layers of isodiametric cells in the central portion of the mesophyll. Prismatic crystals occur in both palisade and spongy parenchyma cells. Large and small vascular bundles imbedded within the spongy mesophyll are sheathed by border parenchyma. The median bundle is not different from other bundles. The general pattern of venation is striate, but the veins running along the longitudinal axis of the leaf are interconnected by small bundles at frequent intervals so that a strongly developed and compact network of veins with many vein islets of varying sizes results. Isolated tracheids with spiral thickenings are found occasionally outside the bundles. Vascular bundles are not accompanied by fibers. Strands of 7–8 collenchyma cells with highly reduced lumens occur along leaf margins under the epidermis.

Gagea arvensis Dum. var. semiglabra Beck (fig. 7) is a bulbous plant occurring commonly in fields, fallow lands and in thickets under the protection of small steppic shrubs. The smooth, flat, lanceolate, light green, tender leaves are 7–8 cm. long, 5–6 mm. wide and 350–380 microns thick. Involution occurs upon wilting, although there are no specialized motor cells.

The epidermis consists of long tabular cells with straight radial walls. The outer tangential walls of epidermal cells are 12–14 microns thick on both surfaces. However, the outer tangential walls of the upper epidermis project and become almost papillate especially in the cells adjacent to the stomata. Apparently the adaxial epidermis is involved in water storage. A finely striate cuticle covers the entire leaf. The stomata are not sunken, and they occur on both the upper and lower epidermis at nearly equal frequencies. The guard cells are 20 microns wide, 45 microns long and 20 microns thick. They are equipped with well developed inner and outer ledges. Subsidiary cells are not present. The long unicellular trichomes occurring along leaf margins are dead, thick walled cells with papillate projections all around them. The leaf structure is dorsiventral, and the mesophyll is provided with a single layer of palisade on the abaxial side. The palisadé parenchyma is poorly differentiated, although sometimes it appears to be biseriate. The greater part of the mesophyll consists of large spongy parenchyma cells, 4–5 cell layers thick. These cells are more or less isodiametric and variable in size, but cells with a diameter of 100–120 microns are not uncommon. The spongy parenchyma cells, with large central vacuoles filled with sap, are mainly responsible for the succulent texture of the leaves. Crystal sand is found in the spongy parenchyma cells, but no specialized idioblasts occur.

Vascular bundles are not accompanied by fibers, but interestingly enough are sheathed by two layers of border parenchyma, thin walled cells which appear round in transectional view. The inner bundle sheath consists of smaller cells than those of the outer bundle sheath. There are no sheath extensions on either side of the bundles. Vascular bundles present a typical striate pattern. They converge near the leaf apex, but interconnecting veinlets have not been observed. They are more widely spaced than in any other species studied. Isolated vascular strands lie parallel to adjacent vascular bundles. These strands consist of a few helical tracheids and terminate in undifferentiated procambial cells at both ends. There is no evidence of bundle sheaths around the isolated vascular strands.

Leaves of *Gagea* do not present striking xeromorphic features. They represent a leaf type at the border line between mesomorphic and xeromorphic structures.

MERENDERA TRIGYNA (Adam) Woron. (fig. 8) is a bulbous plant with strap shaped, flat leaves which are 3–4 mm. wide and 300–350 microns thick. It occurs in the mountain steppe and blooms during February and March. The leaves are isolateral and involution occurs upon wilting.

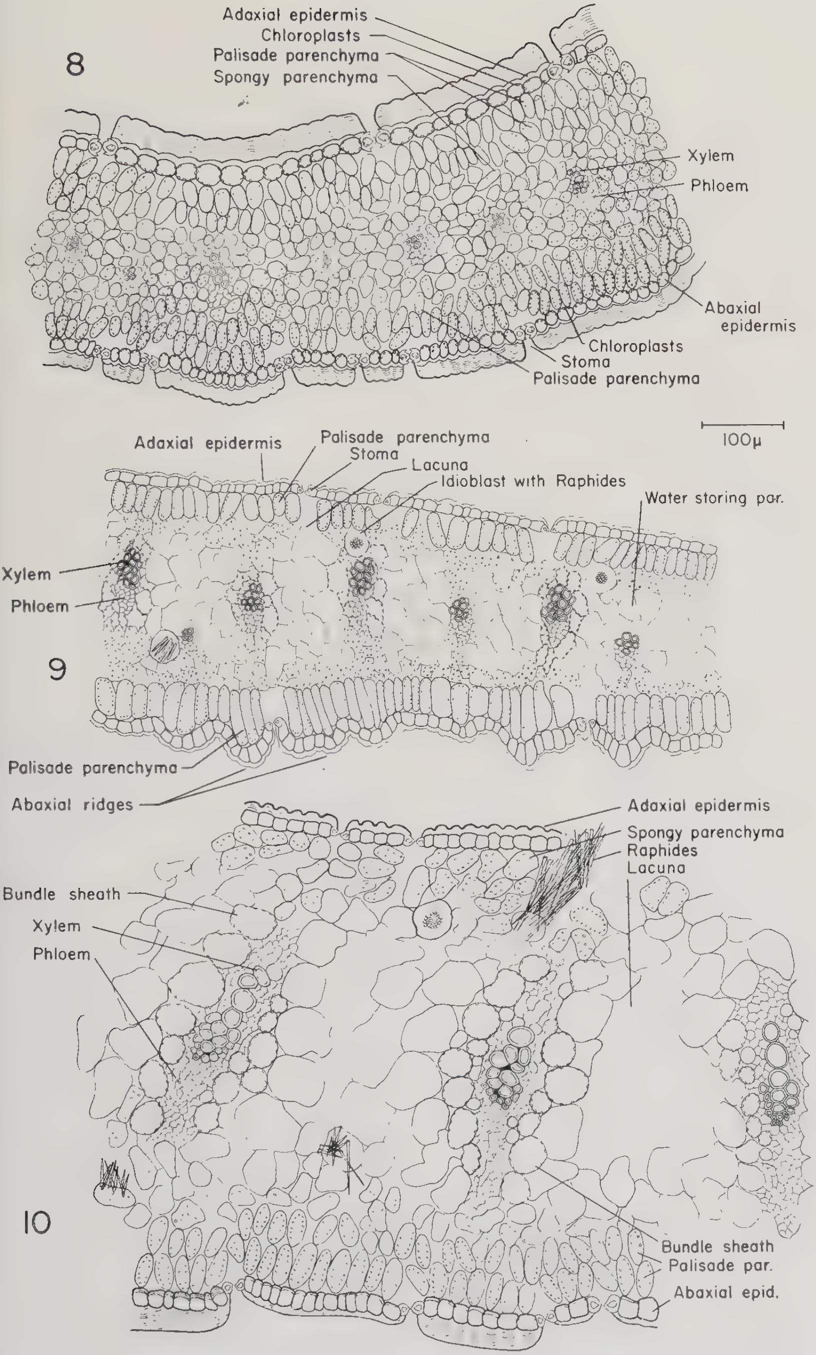
The epidermis consists of rectangular cells, 14 microns wide and 70 microns long. Upper and lower epidermis are coated by a striate cuticle 2–3 microns thick. The outer tangential walls of the epidermal cells are remarkably thick, and cell lumina are extremely reduced. Both upper and lower epidermal cells contain chloroplasts. The stomata are sunken and distributed on both adaxial and abaxial surfaces. Guard cells are 12 microns wide and 32 microns long as seen in face view. Inner and outer ledges are well developed, the outer ones being cutinized. Subsidiary cells are not present. Short unicellular trichomes occur along leaf margins. The cell walls of the trichomes are very thick and appear refringent under polarized light.

The mesophyll has a biseriate palisade on both adaxial and abaxial sides. Palisade parenchyma cells are small and densely arranged. They occupy two thirds of the mesophyll as seen in transverse section. Spongy parenchyma consists of 5–6 cell layers between upper and lower palisade. Crystal sand occurs in spongy parenchyma cells. There are no specialized idioblasts in the mesophyll.

Vascular bundles are closely spaced and transconnections occur very frequently. Border parenchyma cells containing very few chloroplasts are restricted to outer edges of xylem and phloem. Consequently they do not form a continuous sheath around bundles. There are no fibers associated with the vascular bundles, but strands of partially lignified, hypodermal fibers extend along leaf margins.

MUSCARI COMOSUM Mill. (fig. 9) is a bulbous plant which grows in mountain steppe as well as in cultivated lands. Strap-shaped leaves, slightly deflexed at their tips, are 10–15 cm. long, 1–1.5 cm. broad and 250–350 microns thick. Incomplete involution takes place upon wilting.

The upper epidermis is smooth, while the lower epidermis exhibits a wavy surface although there are no ridges on the abaxial side. Epidermal cells are almost prosenchymatous, 10–15 microns wide and 150–200 microns long. The cuticle is thin and the outer tangential walls of the epidermal cells are moderately thick. Stomata occur on both surfaces of the leaves. They are nearly at the same level with the rest of the epidermal cells of the adaxial surface, but the stomata of the abaxial surface are hidden within the furrows caused by the plication of the epidermal



Figs. 8–10. Transverse sections of leaves: 8, *Merendera trigyna*; 9, *Muscari comosum*; 10, *Muscari racemosum*.

tissue on this side. Guard cells are not accompanied by subsidiary cells and there are no trichomes.

Leaves are typically isolateral; mesophyll is provided with a uniseriate palisade on adaxial and abaxial sides. Palisade parenchyma cells are nearly cylindrical in shape and are compactly crowded. Cells of the abaxial palisade are almost twice as long as the cells of the adaxial palisade. Together the two palisade layers occupy about one third of the thickness of mesophyll. Spongy mesophyll consists of 7–8 layers of cells which are loosely arranged, leaving conspicuous intercellular spaces between them. Chlorenchymatous cells are located around vascular bundles and adjacent to the inner edges of the palisade layers. Spongy parenchyma cells, located centrally in the mesophyll, are larger than the cells of the peripheral spongy parenchyma and contain few chloroplasts and large vacuoles. This water storing parenchyma gives a fleshy texture to the leaves. It is interesting to note that this tissue becomes lacunate as the leaves reach maturity. Cylindrical idioblastic cells containing raphides are abundant in the spongy mesophyll.

Vascular bundles are surrounded by a single layer of bundle sheath. Large and small bundles which are distantly spaced and which alternate with each other run along the longitudinal axis of the leaves. Small veins interconnecting the "parallel" veins are common. Sclerenchyma cells are not present.

With the exception of isolateral structure of leaves and presence of water storing tissue, *Muscari comosum* does not present any appreciable xeromorphic feature and lies rather on the mesomorphic side, especially in respect to the presence of lacunae and prominent intercellular spaces and high proportion of spongy parenchyma as compared to the proportion of palisade parenchyma. It can well be regarded as a mesoxeromorphic leaf.

MUSCARI RACEMOSUM Mill. (fig. 10) is a larger bulbous plant than *Muscari comosum* Mill. It grows in the mountain steppe. The leaves are lanceolate to almost ovate, tapering gradually toward apex. They are coated with a waxy substance which gives a glaucous appearance to the leaves. The upper surfaces of the leaves are flat and the lower surfaces are ridged. Involution takes place upon wilting although there are no bulliform cells in the epidermis.

Epidermal cells are prosenchymatous, 18–20 microns wide and 220–280 microns long. The cuticle is thicker than the cuticle of the preceding species. Outer walls of the epidermal cells are very thick and are characterized by lamellate cutinization. The wall thickness is more prominent in the epidermal cells on the abaxial surface than in those on the adaxial surface. Inner tangential walls of the abaxial epidermal cells are also thickened considerably. Portions of the abaxial epidermis beneath vascular bundles have exceedingly thick outer cell walls reaching 25 microns in thickness. These thick-walled epidermal cells contribute to the formation of abaxial ridges on the leaves since there are no hypodermal fibers along ridges. Outer cell walls of the abaxial epidermis adjacent to the mesophyll between vascular bundles are relatively thin walled. Consequently thin and thick walled portions of the lower epidermis alternate with each other following the spacing of vascular bundles and dorsal ridges as seen in transverse section. Stomata are sunken and occur on both surfaces. There are no subsidiary cells or trichomes.

Unlike the previous species, the leaves of *Muscari racemosum* are dorsiventral with a biseriate palisade on the lower side. The central portion of mesophyll is occupied by an extensive water storing tissue which takes up two thirds of the thickness of the mesophyll between vascular bundles. Water storing parenchyma cells contain very few chloroplasts. Assimilatory cells of the spongy parenchyma are situated at the peripheries of the water storing tissue and are very loosely arranged, leaving conspicuous air spaces between them. Sizable lacunae are present in the centers of water storing tissues. Although these lacunae seem to be schizogenous cavities, there is ample evidence for collapsed cell walls, suggesting that they are partly lysigenous in origin (cf. Newcombe 1894). Bizarre idioblasts containing raphide bundles are abundant in the mesophyll.

Vascular bundles are surrounded by bundle sheaths and are devoid of fibers. However, converging bundles of the leaf apex are associated with many tracheoid idioblasts. Vascular bundles are widely spaced, as in the preceding species. Transverse veinlets occur frequently, either connecting the longitudinal bundles or terminating blindly in mesophyll.

The leaves of *Muscari racemosum* also can be considered as mesoxeromorphic, especially considering the presence of large lacunae. This lacunate condition, however, may also be considered as an ancestral feature, if we follow the classical belief that the xeromorphic leaves are derived from mesomorphic leaves during evolution.

Ornithogalum is represented by ten species in the steppic flora. Only two species are considered in this paper.

Ornithogalum armeniacum Bak. (fig. 11) is a bulbous plant which grows in the valleys of the mountain steppe. Linear leaves are 2–3 mm. wide and 250–400 microns thick. The upper leaf surface is flat, the lower one ridged by prominent thickenings of the outer walls of epidermal cells. Involution occurs upon wilting (fig. 11B).

Epidermis is covered by a heavy cuticle. Epidermal cells of both surfaces are more or less tabular in shape, 20–22 microns wide and 247–330 microns long. Stomata are not sunken and occur on both surfaces. Guard cells are thick-walled and equipped with cutinized external ledges only. Guard cells are 13 microns wide and 39 microns long, and are not accompanied by subsidiary cells. Trichomes are not present.

The leaf is isolateral and mesophyll is provided by a uniseriate palisade on adaxial and abaxial sides. It is interesting to note that the adaxial palisade is interrupted by water storing parenchyma cells above the median vascular bundle (fig. 11a and b). Assimilatory parenchyma cells of the spongy mesophyll form one or two layers bordering the palisade layers. The central portion of mesophyll is occupied by water storing parenchyma and schizogenous lacunae. Raphide containing excretory idioblasts are abundant particularly in the spongy mesophyll and along the leaf margins.

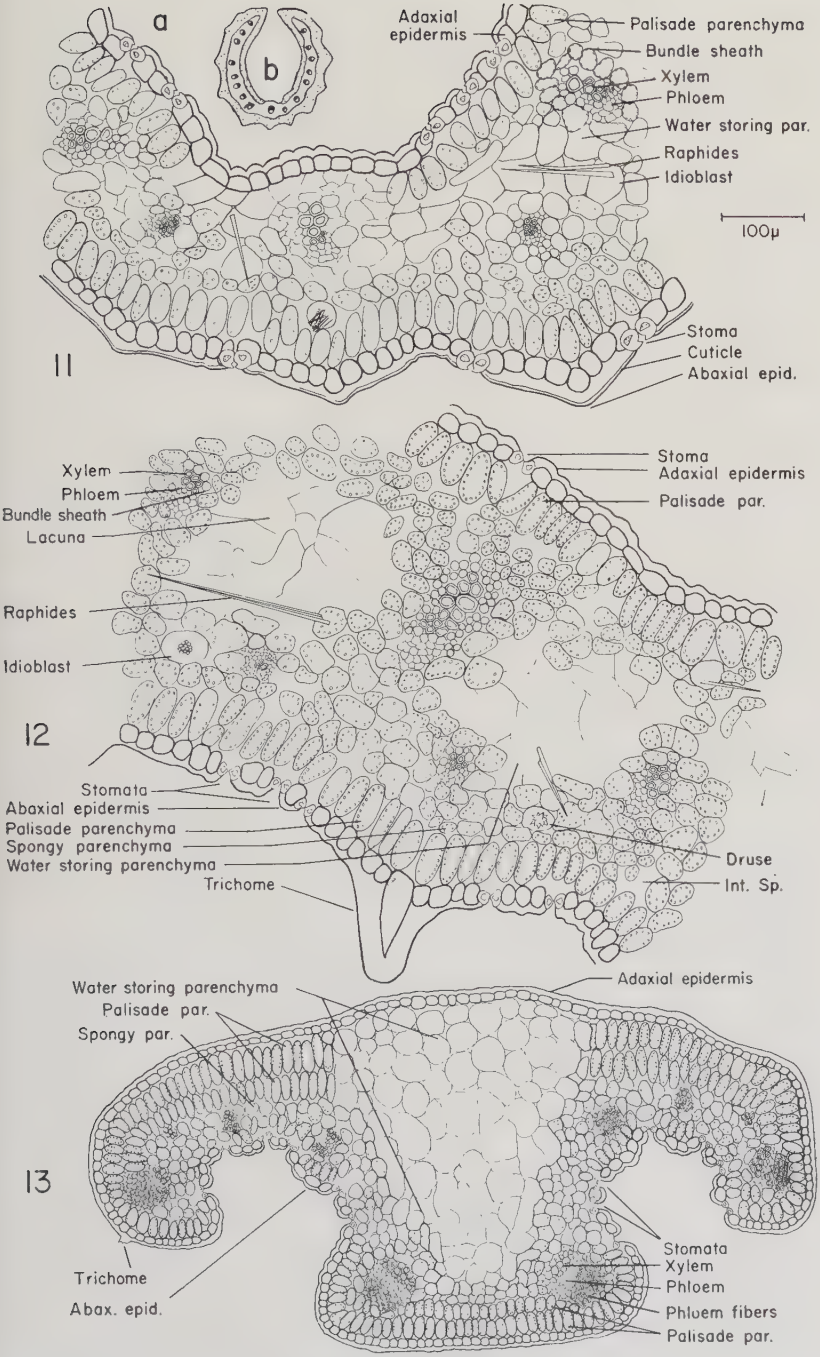
Vascular bundles lack sclerenchyma and are sheathed by bundle sheaths. Large bundles are closer to the adaxial leaf surface than are the alternating small bundles. Transverse veinlets interconnect large "parallel" veins obliquely or perpendicularly, very often without making any contact with the alternating smaller longitudinal bundles.

ORNITHOGALUM NARBONENSE L. var. PYRAMIDALE Boiss. (fig. 12) is a bulbous plant which grows in fields and fallow lands as well as in the mountain steppe. Strap-shaped, fleshy leaves are 20–30 cm. long, 1–1.5 cm. wide and 500–600 microns thick. Upper surfaces of the leaves are flat; lower surfaces are more prominently ridged than those of *O. armeniacum*. Slight involution occurs upon wilting.

The epidermis consists of very narrow cells, tapering toward the ends. Epidermal cells are 618–825 microns long, 25–30 microns wide, and 35–38 microns deep. Superficial walls of the epidermal cells project on both adaxial and abaxial sides. Outer walls of the epidermal cells are thick and heavily cutinized. Stomata are distributed throughout both surfaces of leaves and are sunken distinctly on the lower epidermis. Guard cells are 12 microns wide and 32 microns long; they are not accompanied by subsidiary cells. Two kinds of unicellular trichomes have been observed: very thick walled conical trichomes 100–110 microns long which occur along the abaxial ridges; and cylindrical trichomes 345–450 microns long which are confined to the leaf margins.

Leaves are isolateral and the mesophyll has a uniseriate, well-developed palisade on abaxial and adaxial sides. Again the adaxial palisade is interrupted by a few large cells without chloroplasts along the median groove. These cells may function as motor cells together with other cells between median bundle and epidermal cells lining the groove. Spongy parenchyma is more prominent than it is in the leaves of the preceding species. The central portion of mesophyll is occupied by a water storing tissue which consists of very large irregular parenchyma cells of 4–5 layers. Schizogenous lacunae develop within this water storing tissue in mature leaves. Excretory idioblastic cells containing druses or raphides of calcium oxalate are abundant in spongy mesophyll. Individual raphide crystals are 4–5 microns thick and 206–230 microns long. Very long isolated individual fibers occur in the mesophyll. These fibers are about 20 microns thick and 8–14 millimeters long, extending along the longitudinal axis of the leaf, not far from large vascular bundles.

The vascular bundles are more closely spaced than those of the pre-



FIGS. 11–13. Transverse sections of leaves: 11, *Ornithogalum armeniacum*; 12, *Ornithogalum narbonense* var. *pyramidale*; 13, *Crocus ancyrensis.*

ceding species. Large and small veins are interconnected by small veins which always run into major veins obliquely and never perpendicularly. Bundle sheaths are well developed around large and small bundles.

IRIDACEAE

This family is represented by *Crocus*, *Gladiolus* and *Iris* in the steppic flora. The genus *Crocus*, which has tunicated, fleshy, underground corms, is represented by six species, two of which will be considered in this paper. *Gladiolus* possesses a tunicated corm which is not so deeply buried as the corms of crocuses. *Gladiolus* is represented by a single species. The genus *Iris* is represented by four species in the steppic flora, all of them having fleshy rhizomes which become slightly woody in age.

CROCUS ANCYRENSIS Maw (fig. 13) is an endemic species abounding in the mountain steppe and blooming from February to April. It has very narrow, stiff, dark green and shiny leaves which are not differentiated into petiole and lamina. These leaves, which remind one of pine needles, represent an extremely reduced leaf type among geophytic monocotyledons of the steppic flora. Their length ranges from 5–8 cm., their width is 800–900 microns and their thickness in the middle portion of the leaf, across the dorsal ridge, is 400–450 microns. The transectional outline of the leaf is almost "T"-shaped. Lateral flaps of the leaf are revolute, 120–162 microns thick. Possibly, change of turgor pressure in the abaxial epidermal cells of the lateral flaps is responsible for the revolution mechanism.

The epidermis consists of very narrow and elongated cells which appear almost fusiform in surface view. Epidermal cells are 290–300 microns long, 14–16 microns wide and 18–24 microns deep. The cuticle is 1–2 microns thick and covers the entire leaf surface. Both outer and inner tangential walls of the epidermal cells are strongly thickened, the outer walls being much thicker than the inner ones. The lumina of the epidermal cells are highly reduced, particularly along the margins of the lateral flaps of the leaf. The stomata are sunken and appear on the abaxial surface of the foliar flaps and along the upper portions of the thickened abaxial ridge of the leaf. The adaxial surface of the leaf and the abaxial surface of the dorsal ridge are devoid of stomata. Guard cells are very small, 7–8 microns wide and 18–20 microns long. Very few unicellular trichomes occur along the margins of foliar flaps and along lateral corners of the dorsal ridge.

Leaves are isolateral in a peculiar way. A strongly developed, biseriate palisade consists of small and tightly arranged cells. Palisade is interrupted by water storing parenchyma cells on the adaxial side. Spongy mesophyll is differentiated into assimilatory and water storing tissues. Small chlorenchymatous cells of the spongy mesophyll form 2–5 rows in foliar flaps as well as in dorsal ridge, beneath palisade parenchyma. The central portion of the mesophyll is occupied by water storing tissue which extends from the dorsal ridge to the adaxial epidermis in a "V"-shape as seen in transectional view. Water storing parenchyma cells lack chloroplasts. They appear as a white band on the adaxial sides of the leaves. Crystals and idioblasts are not present.

Vascular bundles are strongly developed and run very close to each other and to the abaxial epidermis. A median bundle is not present. Each foliar flap and each "corner" of dorsal ridge is provided with a major bundle which is characterized by the presence of a well-developed bundle cap. Minor bundles have small amounts of phloem fibers or none. The minor bundles anastomose highly and interconnect the major bundles. Xylem fibers are not present and bundle sheaths are not clearly differentiated.

CROCUS SUTERIANUS Herb. (fig. 14) is another endemic species which occurs in the mountain steppe of Asia Minor. It has a spherical corm protected by a fimbriate tunic. The leaves are linear, 10–15 cm. long, 2–3 mm. wide and 200–300 microns thick in foliar flaps. With the exception of a white adaxial stripe, the leaves are dark green and stiff. The dorsal ridge is more pronounced than that of the preceding species and the transectional outline of the leaf is T-shaped (fig. 14b). The foliar flaps are revolute and roll backwardly upon wilting. Ridged middle portion of leaves is 1–1.5 mm. thick, which is twice or three times as thick as that of *Crocus ancyrensis*.

Epidermal cells, which are very slender and fusiform as seen in face view, are 130–243 microns long, 20–26 microns wide and 25–28 microns deep. The entire leaf surface is covered by a thick cuticle which reaches a thickness of 4 microns on the adaxial epidermis and on the abaxial epidermis of the dorsal ridge. Inner and outer tangential walls of the epidermal cells are very thick. Abaxial epidermal cells of foliar flaps are characterized by dome-shaped outer walls. These highly vacuolated cells are relatively thin-walled and may function as motor cells. Stomata are sunken and restricted to the abaxial epidermis of foliar flaps and to the lateral sides of the dorsal ridge. Guard cells are very small, 14 microns long and 7 microns wide. There are no subsidiary cells. Unicellular, dead trichomes occur only along the margins of the foliar flaps. Trichomes are 120 microns long and 15 microns thick.

The leaves are peculiarly isolateral as described in the preceding species. The adaxial palisade consists of narrow cylindrical cells which are tightly arranged and biseriate, but the cells tend to be in three layers near water storing tissue. The palisade tissue is strongly developed at the expense of spongy parenchyma in the foliar flaps and occupies more than half of the thickness of the mesophyll. Again the spongy mesophyll is differentiated into assimilatory and water storing tissues (fig. 14a and b) as described for *Crocus ancyrensis*. Assimilatory spongy parenchyma cells are small, tightly arranged and form four layers on the abaxial side of the foliar flaps and in dorsal ridge. Water storing parenchyma cells are large and have prominent air spaces between them. Idioblasts containing large prismatic crystals are abundant in the assimilatory spongy tissue. These crystals are 15–16 microns thick and 97–146 microns long. The idioblasts are situated around the bundle caps and occasionally occur also "scattered" within the assimilatory spongy mesophyll.

Vasculation of the leaves is similar to that of *Crocus ancyrensis* with minor differences. The major bundles along the margins of foliar flaps and those at the "corners" of the dorsal ridge are accompanied by xylem and phloem fibers. Furthermore, the bundle sheaths are more distinctly differentiated and the vascular bundles more compactly arranged than those of *C. ancyrensis*.

GLADIOLUS ATROVIOLACEUS Boiss. (fig. 15) is a cormous plant 30–55 cm. high. It has a wide distribution in the Middle East. It grows in fields, fallow lands as well as in mountain steppe. The leaves are strap-shaped, firm, strongly ribbed, 15–20 cm. long, 4–5 mm. wide and about 0.5 mm. thick. From the morphological point of view, these leaves present a very peculiar structure. Typically, the leaves are unifacial, with inverted bundles, but the presence of two marginal bundles and a prominent marginal groove (fig. 15a and b) along one edge of the blade and the presence of a single bundle with a well developed ridge along the other edge of the blade suggests the folding and fusion of two halves of the blade during ontogeny. However, there is no evident line of fusion in the mesophyll. The problem may be solved by an ontogenetic study. Corms are ovoid, tunicated and buried superficially in ground.

If the interpretation of the foliar structure given above be true, the epidermis of upper and lower leaf surfaces may represent the abaxial epidermis only. The epidermal cells are tabular in form, 48 microns long, 30 microns wide and 20 microns deep. The cuticle is 2 microns thick on the blade surface and 4–5 microns thick along leaf margins. Epidermal cells form 2–5 papillose projections. Stomata are sunken and occur on both leaf surfaces. Epidermis of the projecting ribs has no stomata or trichomes.

The leaves are isolateral in the sense that abaxial and adaxial sides of the leaves present identical structure, but the mesophyll is not differentiated into palisade and spongy parenchyma. The mesophyll consists of very small, tightly arranged, elliptical cells which resemble palisade, but they lie parallel to the leaf surface. Water storing parenchyma cells are situated between opposite major ribs of the blade (fig. 15b). Idioblasts containing prismatic crystals are distributed at random within mesophyll. Crystals are 16 microns thick and 65–160 microns long. Tracheoid idioblasts occur commonly in mesophyll.

Major vascular bundles are accompanied by bundle caps and project on leaf surfaces as well as along leaf margins. Major bundles extend "parallel" but the minor bundles which are imbedded in mesophyll anas-

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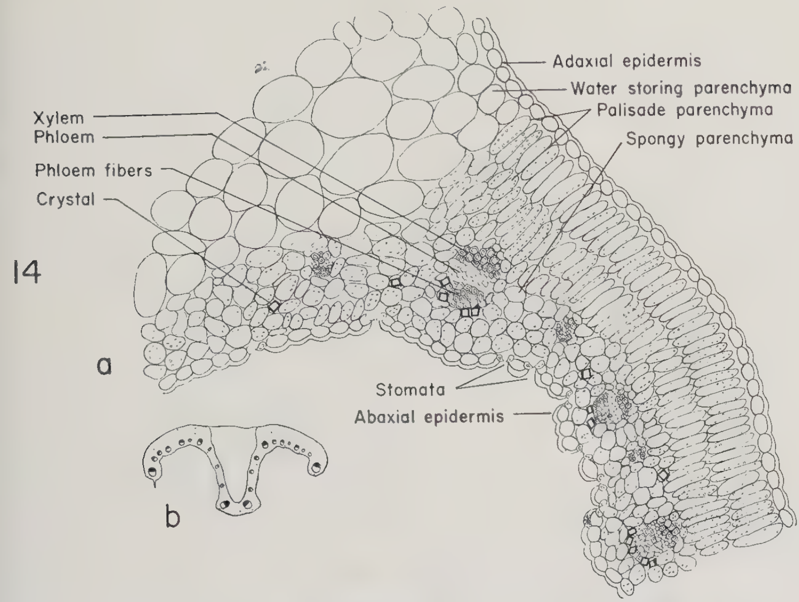

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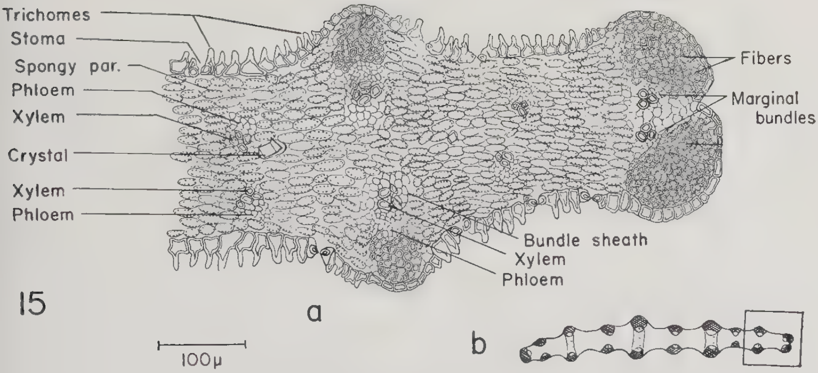


FIGS. 14–15. Transverse sections of leaves: 14, *Crocus suterianus*; 15, *Gladiolus atroviolaceus*.

tomose frequently and interconnect the major bundles. Minor bundles lack fibers and are surrounded by bundle sheaths. As a whole, the leaves present a compact vascular system.

IRIS APHYLLUS L. (fig. 16) is a rhizomatous plant occurring in the mountain steppe and in the openings of forest remnants of the steppic region. Bluish-green, sword-shaped, erect leaves are 10–15 cm. long, 1–1.5 cm. broad and 800 microns thick in the lower sheath portion, 400 microns thick in the upper blade portion. Unifacial structure of leaves with inverted vascular bundles is seen clearly (fig. 16a, b, and c).

Epidermal cells are 227 microns long, 48 microns wide and 39 microns deep and rectangular in form. Stomata are sunken and occur on both surfaces of the blade. However, there are no stomata on the adaxial epidermis of the flaps in sheathing lower portions of leaves. Considering the development of these unifacial leaves, it is understandable that a similar epidermis occurs all around the upper blade portions of leaves; therefore the actual distribution of stomata would be confined to abaxial epidermis only. The guard cells are typically reniform, 50 microns long and 25 microns wide. There are no subsidiary cells. Unicellular, thick walled trichomes occur on the abaxial epidermis only and there are no trichomes on the adaxial epidermis of sheathing flaps. The trichomes are 40 microns long and conical in shape.

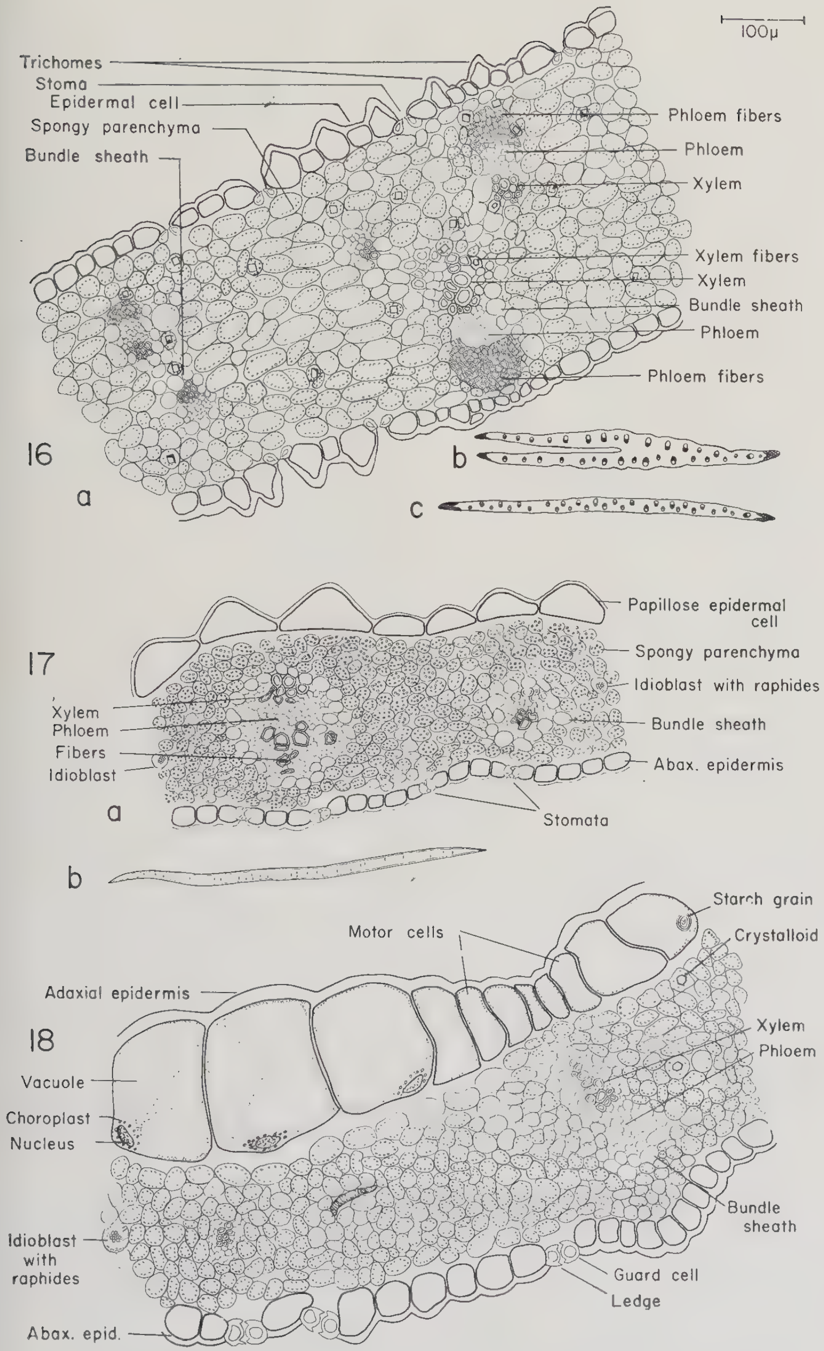
The blades are isolateral in the sense that both sides of the blades are similar in regard to uniform mesophyll and inverted bundles, although there is no palisade tissue. On the other hand sheathing flaps present a dorsiventral structure since mesophyll is differentiated into water storing parenchyma on the adaxial side and assimilatory parenchyma on the abaxial side. Furthermore xylem tissues of vascular bundles face the adaxial epidermis in sheathing flaps (fig. 16b). The mesophyll of the blade consists of elliptical spongy parenchyma cells lying with their longitudinal axes parallel to leaf surfaces. This is quite similar to the situation found in *Gladiolus* leaves except that the parenchyma cells in *Iris* leaves are at least twice as big as the assimilatory parenchyma cells of *Gladiolus* leaves. Extensive water storing tissue occupies the central part of the mesophyll in lower sheathing portions of leaves. Idioblasts containing prismatic crystals are abundant in mesophyll. These crystals are very similar to those found in the leaves of *Crocus suterianus* and *Gladiolus atroviolaceus*.

Vascular bundles of the leaves are strongly developed, but are not as compact as the bundles in *Crocus* and *Gladiolus* leaves. The bundle caps also are strongly developed along major veins, but do not project as ribs on the leaf surface. Xylem tissues of the major veins possess a few fibers. Phloem fibers are lignified while thick walls of xylem fibers do not show any sign of lignification. Veinlets interconnecting the major bundles occur frequently. Some of the veinlets terminate blindly in mesophyll and very often are associated with tracheoid idioblasts at their tips. Strands of fibers occur along the margins of sheathing blades as well as along both edges of blades (fig. 16b and c).

ORCHIDACEAE

This family is represented by a number of terrestrial orchids which grow in moist places of the steppic region. The specimens of *Limodorum abortivum* and *Orchis mascula* subsp. *pinetorum* were collected from an open pine forest in Beynam at an altitude of 1450 meters.

LIMODORUM ABORTIVUM (L.) Sw. (fig. 17) is a saprophyte with well developed fleshy rhizomes. Scale-like leaves are small, very tender and nearly surround the scape. Apical portions of these leaves slightly diverge



FIGS. 16–18. Transverse sections of leaves: 16, *Iris aphyllus*; 17, *Limodorum abortivum*; 18, *Orchis mascula* subsp. *pinetorum*.

from the scape and form a short blade about 2–3 cm. long, 1 -1.5 cm. broad and 250–300 microns thick. Involution occurs slightly upon wilting.

The adaxial epidermis consists of large tabular cells with papillose outer walls. Water storage takes place in upper epidermis. The abaxial epidermis consists of much smaller cells than those of the adaxial epidermis. Stomata occur on the abaxial epidermis only and are not sunken. Guard cells are 65 microns long and 23 microns wide. Each stoma is surrounded by six subsidiary cells, each guard cell being subtended by three of them. The presence of four *Tradescantia*-type subsidiary cells was reported by Solereder and Meyer (1930) in some orchidaceous genera. The radial walls of subsidiary cells extend toward the stomatal opening, the stomatal apparatus as a whole resembling a rosette in face view.

Mesophyll is not differentiated into palisade and spongy parenchyma and consists of more or less uniform isodiametric parenchyma cells arranged tightly. Patches of tracheoid idioblasts, fibers and mucilage- or raphide-containing excretory idioblasts are present in mesophyll. The occurrence of such a great variety of idioblasts together in one species was not observed in other species of the present study.

Major vascular bundles present a striate pattern, but minor bundles anastomose frequently and form also peculiar zigzags extending back and forth and interconnecting major bundless eventually.

ORCHIS MASCULA L. subsp. PINETORUM Boiss. (fig. 18) has tuberous fleshy roots protected by a dark brown cork tissue. The leaves are basal, flat and very tender, 10–15 cm. long, 1.5–2 cm. wide, 350-450 microns thick. Upper leaf surface is grooved along the median bundle and the lamina halves fold over along the median bundle when a water deficit develops.

The adaxial epidermis consists of remarkably large tabular cells 340–550 microns long, 100–150 microns wide and 120–200 microns deep. These cells are characterized by thick outer walls, peripheral cytoplasm and large vacuoles. Their nuclei are pushed against inner tangential walls. They contain chloroplasts and concentric starch grains. Epidermal cells along the adaxial groove are specialized as motor cells and are much smaller than adjacent water storing epidermal cells. Adaxial epidermis is mainly responsible for the fleshy nature of the leaves. The occurrence of water storing epidermis was reported by Metzler (1924) for other orchidaceous genera such as *Dendrobium, Otochilus, Pholidota* and *Pleione.* The abaxial epidermis consists of much smaller cells. Stomata occur on the abaxial epidermis only and are not sunken. Guard cells are 70 microns long, 35 microns wide and are equipped with strongly developed inner and outer ledges. Subsidiary cells and trichomes are not present.

Mesophyll consists of small isodiametric parenchyma cells which are arranged rather tightly. Idioblasts containing protein crystalloids (Kuester 1935) and raphide bundles associated with mucilage occur at random in the mesophyll. There is no sclerenchyma, but a strand of a few hypodermal collenchyma cells occurs occasionally on the dorsal side of the ridge.

Vascular bundles are widely spaced. Major and minor veins anastomose frequently. Bundle sheaths are differentiated distinctly around major bundles.

The leaves of *Limodorum abortivum* and *Orchis mascula* subsp. *pinetorum* do not show striking xeromorphic features with the exception of folding of blades, epidermal water storage, compactness and decreased cell size in the mesophyll, and abundance of excretory idioblasts. On the other hand they exhibit a prevailingly mesomorphic structure, and may be considered as mesoxeromorphic.

The present study shows that not all xeromorphic characters occur universally in the leaves of the geophytic monocotyledons investigated. Each plant exhibits a different combination of xeromorphic features. Furthermore, there are quantitative differences in the degree of development of each particular xeromorphic feature. I believe many of these xeromorphic characters are genetically fixed as the result of a natural selection in this semi-arid environment. Consequently these plants are morphologically and physiologically adapted to tolerate the factors of the environment. Drought is one of the most severe factors and the plants in question are well adapted to survive drought. On the other hand some of the features described may represent xeroplastic characters which may be subject to qualitative and quantitative changes under varied conditions of the environment. It would be very desirable to conduct an experimental study using controlled conditions to determine the extent of plasticity of the foliar xeromorphic features.

SUMMARY

The foliar histology of eighteen species of geophytic monocotyledons representing Araceae, Liliaceae, Gramineae, Iridaceae and Orchidaceae has been described. The research materials were collected wholly from the central Anatolian steppic region. They exhibit certain uniformities such as geophytism, shallow root distribution, leaf shape, osmotic concentrations, and phenological periodicity.

Xeromorphic characters observed in gross morphology and in anatomical structure do not occur universally in the leaves of all plant species studied, but each species exhibits combinations of certain foliar xeromorphic features as follows. Reduction of the leaf surface: *Allium stamineum, Crocus ancyrensis, C. suterianus*; revolute margins: *Crocus ancyrensis, C. suterianus*; unifacial leaves: *Allium rotundum, A. stamineum, Gladiolus atroviolaceus, Iris aphyllus*; involution or folding of blade upon wilting: *Hordeum bulbosum, Poa bulbosa, Allium rotundum, Colchicum biebersteinii, Gagea arvensis, Merendera trigyna, Muscari comosum, M. racemosum, Orchis mascula*; increased thickness of the blade: *Allium stamineum, Crocus ancyrensis, C. suterianus*; strong cutinization of epidermis: *Allium rotundum, A. stamineum, Colchicum biebersteinii, Gagea arvensis, Merendera trigyna, Muscari racemosum, Ornithogalum armeni-*

acum, O. narbonense, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus; increased thickness of the epidermal cell walls: *Allium rotundum, A. stamineum, Colchicum biebersteinii, Merendera trigyna, Ornithogalum armeniacum, O. narbonense, Crocus ancyrensis, C. suterianus, Orchis mascula*; depression of stomata: *Poa bulbosa, Allium rotundum, A. stamineum, Merendera trigyna, Muscari racemosum, Ornithogalum narbonense, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus, Iris aphyllus*; the occurrence of trichomes: *Allium stamineum, Gagea arvensis, Merendera trigyna, Ornithogalum narbonense, Crocus suterianus, Gladiolus atroviolaceus, Iris aphyllus*; epidermal water storage: *Gagea arvensis, Limodorum abortivum, Orchis mascula*; isolateral leaf: *Allium rotundum, A. stamineum, Colchicum biebersteinii, Merendera trigyna, Muscari comosum, Ornithogalum armeniacum, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus, Iris aphyllus*; strongly developed palisade parenchyma at the expense of spongy parenchyma: *Allium stamineum, Merendera trigyna, Ornithogalum armeniacum, Crocus ancyrensis, C. suterianus*; compactness of the tissues: *Poa bulbosa, Allium rotundum, Merendera trigyna, Crocus ancyrensis, C. suterianus*; decreased size of cells: *Poa bulbosa, Allium rotundum, Merendera trigyna, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus, Orchis mascula*; water storing tissue in mesophyll: *Allium rotundum, A. stamineum, Gagea arvensis, Muscari comosum, M. racemosum, Ornithogalum armeniacum, O. narbonense, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus, Iris aphyllus, Limodorum abortivum*; relative compactness of vascular bundles: *Hordeum bulbosum, Poa bulbosa, Allium rotundum, Colchicum biebersteinii, Merendera trigyna, Ornithogalum narbonense, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus*; strongly developed fibers: *Hordeum bulbosum, Poa bulbosa, Allium rotundum, Crocus ancyrensis, C. suterianus, Gladiolus atroviolaceus, Iris aphyllus.*

The leaves of *Arum orientale, Gagea arvensis, Muscari comosum, Limodorum abortivum* and *Orchis mascula* have been designated as mesoxeromorphic, since they exhibit structural features intermediate between mesomorphic and xeromorphic leaves.

In spite of the adaptive responses of any particular tissue to the xeric environment, the anatomical structures of the monocotyledonous leaves studied are highly specialized and the pattern of tissue organization is quite distinct even between species of the same genus.

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REVIEWS

Die Evolution der Angiospermen. Von Professor Dr. Armen Takhtajan, Leningrad. Aus dem Russischen übersetzt von W. Höppner, Berlin. viii + 344 pages, 43 figures. VEB Gustav Fischer Verlag, Jena. 1959.

The review of this book by our fellow-member of the California Botanical Society, Dr. Lincoln Constance (Science 132:801. 1960), led me to order it from Messrs. Stechert-Hafner. It is not available in this country. Sent from East Germany, it arrived in about three months, with a bill for $11.65, including postage.

About two thirds of the work may be described as prolegomena. The workings of evolution in general are described; as details, the frequency of neoteny (this term is distinguished from *paedomorphosis*, and preferred to it), and of parallel development, are noted; the hypothesis of a profound difference in mechanism between macroevolution and microevolution is denied. The generally accepted hypotheses as to the usual directions of evolution in the plant body, the xylem, phloem, vascular anatomy of the node, the leaf, the flower and its parts, the fruit and seed, are duly set forth. The telome theory, which denies the foliar nature of stamens and carpels, is rejected.

The flowering plants are held to be genuinely a natural group, being of a single evolutionary origin. The original flowering plants are believed to have been large-leaved trees of tropical mountains.

Surely, the original flowering plants were homoxylous, i.e., without vessels in the wood. The plants now living which are homoxylous as a primitive character (Lemnaceae, at least, are homoxylous by reduction) are primitive in all of their characters. Nevertheless, these few appear to be related to widely divergent heteroxylous groups. Takhtajan suggests the independent origin of vessels in at least five distinct lines of descent. Winteraceae, allied to Magnoliaceae, appear to represent the origin of the bulk of the dicots. Trochodendraceae and Tetracentraceae appear to lead into Amentiferae, and *Amborella* and *Sarcandra* into minor lines. The Nymphaeaceae appear to represent the ancestry of the monocots. Thus certain hypotheses maintained by Bailey and Cheadle are at the same time applied and convincingly supported: the presentation is *elegant* in the sense in which our mathematical and physical colleagues use the term.

Referring primarily to the body of opinion which has just been sketched, Constance remarks, "If in all this there is very little that is startlingly new to Western students of plant evolution, it is interesting to discover that the climate of opinion is not radically different between East and West." I think that there is something more to say. The Russian botanists know everything that we know; Takhtajan cites Bailey and Cheadle, Gundersen and Cronquist. We, on the other hand, can not be certain that political and linguistic barriers have not withheld from us much pertinent information. How many American botanists have cited Koso-Poljansky?

These same opinions of Takhtajan are available also in two essays which have been translated into English by Mrs. Olga Hess Gankin, edited by G. Ledyard Stebbins, published by the American Institute of Biological Sciences, and reviewed by Constance, along with the book, as cited above. In one of these translations, the mere skeleton of Takhtajan's system of the flowering plants is included as an appendix.

In the book, Takhtajan's conception of the phylogeny and the system of the flowering plants constitutes the remaining one-third of the text. The extent of this presentation makes possible a statement of the reasons which have guided him in the placement of each family. I did not note among the prolegomena a statement that no division of the flowering plants into major natural groups, beyond the distinction of dicots and monocots, can be made by any small number of definite characters; that among apetalae, choripetalae and sympetalae, between woody plants and herbaceous, or in any similar system, at least some of the groups are artificial. Neither did I find the correlative statement, that the true system is perceived by recognizing the connections between groups, no matter what may be the characters which indicate these connections. Without stating these principles, Takhtajan has evidently been guided by them. Some years ago, I dared predict that the main outlines of the natural system of the flowering plants would become essentially completely known within our lifetime. I consider that Takhtajan has essentially fulfilled this prediction. Delaying discussion of the taxonomic pattern which he has produced, I shall sketch the phylogeny as Takhtajan sees it, interpolating remarks, among which only the few references to plants which I have personally studied have any claim to authority.

As noted, Takhtajan derives the Amentiferae from something of which the Trochodendraceae and Tetracentraceae are the surviving representatives; these being immediate derivatives of the unknown original flowering plants. The Hamamelidaceae-Platanaceae group is an important secondary center among the Amentiferae, which include also the Juglandaceae and associated families, and the odd monotypic American family Leitneriaceae.

Lauraceae and their allies, including *Amborella*, and the Englerian Piperales, including *Sarcandra*, are treated as minor lines of descent as ancient as any among flowering plants; and Aristolochiaceae (among which the most ancient have apocarpous flowers), with associated families, are treated as another such line.

The remainder of the Englerian Ranales (Winteraceae, Magnoliaceae, Ranunculaceae, Berberidaceae, etc.) lead to the remainder of the dicots. A first offshoot includes the Centrospermae (including Cactaceae) and Papaveraceae.

Starting again from Ranales, the Dilleniaceae-Theaceae group is recognized as a second node in the main line of descent of the dicots. Offshoots at this node include Ericales, Ebenales, a wide range of Parietales (including Salicaceae), and Malvales, with Euphorbiaceae in the same neighborhood.

I was surprised to find Cyrillaceae in Ericales. Cyrillaceae have many of the characters of Bicornes, but seemed excluded by formal characters, notably by the presence of a typical endothecium in the anthers. Takhtajan's Ericales is an extended group, including, with the authority of Schnarf, Saurauiaceae and Actinidiaceae. It now seems to me that if he had placed Cyrillaceae near these families, rather than near Empetraceae, he would have given satisfactory expression to the apparent relationships.

Capparidaceae and Cruciferae are placed near the Parietales. I would have thought that Eames' study of carpels had fixed the position of these families near Papaveraceae.

From the Dilleniaceae–Theaceae group, the main line of descent of the dicots goes on to a third note in Rosales *sensu lato*. From this group spring (1) Myrtales; (2) Rutales-Sapindales-Geraniales-Polygonales (I question this last); (3) Umbelliflorae; and (4) Celastrales-Rhamnales-Santalales. The great family Proteaceae, rather strange to us, is placed near Santalaceae. Since the Proteaceae have simple pistils, this association appears mistaken.

It is generally agreed that the bulk of the Sympetalae—the old orders Contortae, Tubiflorae, Rubiales, and Campanulatae—belong together. Cronquist treated them so. Without strongly committing himself, he appeared disposed to derive them from the Dilleniaceae–Theaceae group. Takhtajan derives them from the neighborhood of Celastraceae. To us, to whom Celastraceae are known merely by cultivated plants of *Euonymus japonica*, the connection is not evident.

A system of the monocots—derived from Nymphaeaceae, these in turn having as old an origin as Amentiferae, Laurales, Piperales, and the main line of the dicots—is duly set forth.

So much for Takhtajan's conception of the phylogeny of the flowering plants, in which only some three or four points have appeared to call for serious question. We shall not abandon detailed studies of species and groups; I expect, however, that the results of these studies will tend to strengthen the hypotheses of relationship which Takhtajan has set forth very much more frequently than they will tend to weaken them.

In the taxonomic expression of his phylogenetic hypotheses, Takhtajan has divided several families; recognized numerous orders of few families (of dicots and monocots together, he has provided eighty-two orders, grouped in eighteen superorders); and designated every order by the stem of a generic name with the termination *-ales*. These practices are the current style or mode-trend. I deprecate them. Is a well-founded opinion, that some two or three families belong together, of sufficient significance to require expression in the category of orders? On most occasions, I think not; what we wish to know of each family is to what group of a dozen or more families it belongs. And as to names, to write Theales (or Guttiferales), Ericales, Malvales, or Gentianales, is to contribute to erasing from memory some of the facts of history, namely that these groups were known, during a period of a century or more, as the orders Guttiferae, Bicornes, Columniferae, and Contortae.—HERBERT F. COPELAND, Sacramento City College, Sacramento 22, California.

Blakeslee: The Genus Datura. By AMOS G. AVERY, SOPHIE SATINA, and JACOB RIETSEMA. xli+289 pp., frontispiece, 67 figs, 34 tables. The Ronald Press Co., New York, 1959. $8.75.

This volume is a monumental review of investigations on the genus *Datura*. The authors, all collaborators of Dr. Alfred Francis Blakeslee, internationally recognized expert in genetics and leader of a devoted group of associates, have given a complete account of more than 40 years of scientific research on this justly famous genus. Focused on genetical studies, the research program was one of the broadest and most complete ever made of plants comprising a single genus. Included is a complete *Datura* bibliography of the 228 published papers of Dr. Blakeslee and associates. An interesting feature is a historical review of the taxonomy of the genus including descriptions, figures, and notes on the ten known species included in the sections *Stramonium, Dutra,* and *Ceratocaulis*. Section *Brugmansia,* regarded by many taxonomists as a a separate genus, is not considered. The sole published summary of the *Datura* nomenclature from 1753 is also included. Nearly 1,400 collections of *D. stramonium,* the most widely investigated species, from many localities scattered all over the temperate zones were grown and studied.

The advanced student of genetics and the tyro alike should find much of interest in the preface, the foreword, and the historical review. The former will be reminded of the tremendous contributions to our understanding of fundamental genetical phenomena made through the investigation of one genus, of the ramifications which result from following up promising leads, and of the influence these researches have had on subsequent biological thinking and experimentation. If the tyro reads no more than the historical review by A. G. Avery, with its account of the medical, ceremonial, and cultural influences of this widely known solanaceous genus, his imagination should be stimulated. He should come away with an appreciation of the depth of genetical roots as he visualizes Kolreuter, Gaetner, Naudin, Godron, de Vries, and Bateson at work on these puzzling plants. In this account, as well as in Dean Sinnott's biographical sketch of Dr. Blakeslee, the career of a distinguished teacher, organizer, and investigator stands revealed in a stimulating manner, while attention is drawn to a magnificent cooperative venture.

A short chapter on the alkaloids of *Datura* by Edward Leete refers to the chemistry, distribution, pharmacology, and biogenesis of these useful substances and clearly indicates the need for further information at both practical and theoretical levels.

For many readers the chapters on "Chromosome Number and Morphology," "Polyploidy," and "Extra-Chromosomal Types" will strike responsive chords. They will be reminded of the use of Belling's iron-acetocarmine technique, of plant breeding methods, of the production of induced polyploids, and of the use of cold, injury, radiation, growth substances, and various other chemicals, including the pioneering work on the use of colchicine, as aids in experimentation. Interesting and valuable ideas were developed through combined cytological and genetical examination of the polyploids and extra-chromosomal types. Segmental interchange and ring formation, comparisons of the effects of single additional chromosomes with the duplication of complete sets of chromosomes, and the evolution of genetic systems come readily to mind as one flips the pages concerned with the details of these and other important phenomena.

Only two allelomorphic pairs of characters had been described prior to 1919 when Blakeslee and Avery reported the first of numerous mutations observed by the Cold Spring Harbor group. The total number of known gene pairs approaches 550 and, among plants, is probably exceeded only by those in *Zea*. These mutations affect all parts of the plant, have appeared either spontaneously or, more often, as a result of a variety of treatments, and are discussed at some length in the chapter on "Gene Mutations." Because of the enormous amount of work required, relatively little attempt was made to locate most of the genes. Nevertheless, genes responsible for 81 distinct mutations representing twelve linkage groups have been located. Methods for constructing maps of the several chromosomes are described. Certain markers have been very useful in various investigations of particular interest, including those investigations affecting male and female sterility.

Miss Satina's short, compact, and beautifully illustrated and organized chapter on "Chimeras" deserves careful reading. Here emphasis on the advantage of utilizing chimeras for obtaining information on the histogenesis of plant structures merits reiteration. The controversy on the origin, nature, and organization of apical meristems and other initials has engaged the attention of many botanists over a long period of years. Perhaps further study of chimeras along the lines suggested by the *Datura* work will help elucidate this perennial problem and will also offer evidence for the diverse functions of the epidermis which have been suggested. The use of periclinal chimeras as a tool in investigating a variety of morphogenetic problems should receive wider recognition.

A chapter on "Radiation Experiments" by A. G. Avery and Jean Cummings gives considerable detail on both methods and results. In this review, already becoming too lengthy, the chapter summary seems to be an efficient device for giving its essence:

> In *Datura,* as in so many other organisms, radiations have been very useful as inducers of genic and chromosomal mutants, and these in turn have been helpful in clarifying the answers to many questions of morphogenesis and physiology. On the other hand, it has been possible to use the knowledge gained from irradiated plants in the comparison of the effectiveness of different types of radiations—thermal and fast neutrons from various sources. To a great extent the conclusions seem clear-cut. All the radiations so far tested seem to cause the same types of both genic and chromosomal aberrations, but the effectiveness of the different radiations is quite different. Neutrons cause much greater effects, both genic and chromosomal, than do either x-rays or gamma rays for equivalent energies.

Geneticists have long since learned the need for a thorough knowledge of the life history of any experimental organism and the *Datura* team is no exception. Clear descriptions of the growth and activity of the tissues associated with reproduction, fertilization, and of the development of the embryo, endosperm, and seed coats are given by Satina and Kietesema in chapters 10 and 11.

"Barriers to Crossability: Prefertilization" and "Barriers to Crossability: Postfertilization" are two important chapters full of suggestions for future research. An inventive and imaginative approach to many experimental problems is presented.

Extensive studies of pollen viability, germination, and pollen-tube growth are summarized. The fate of embryos and endosperm in incompatible crosses, the growth of ovular tumors, and the physiological aspects of seed abortion are among the topics discussed.

In later years special attention has been paid to the vital link between generations, the seed. Problems of incompatability, sterility, and abortion required attention and led to the development of a method for the culture of embryos. Many observations have led to a partial understanding of the numerous complex processes going on simultaneously in the growing seed. Here are dozens of unsolved problems for which the *Datura* investigators suggest promising lines of attack.

In the chapter on "Segmental Interchanges and the Species Problem," Miss Satina assembles considerable material on prime types, racial differences, interspecific hybrids, and the characteristics of hybrids from incompatible crosses. The problems of chromosome analysis, ring formation, and of chromosome-end arrangements are examined. The abundant occurrence of segmental interchange present in the various races of *Datura* is unusual, but the condition is known in some other plants. In spite of intensive study, the exact relationship of the phenomenon to speciation remains obscure. We may agree with Blakeslee when he says that, "The frequency of interchange of chromosomal fragments in *D. stramonium* and the relation of this phenomenon to the formation of new pure-breeding types has led to the hypothesis that segmental interchange has accompanied the changes responsible for the formation of species in the genus *Datura*. Nevertheless, in spite of very intensive study the relationship of the phenomenon to speciation remains obscure." We may hope that some day *Datura* will be a valuable instrument in helping us work out the relationship between genes and chromosomes which will further our understanding of the evolutionary picture.

The scientific world owes its gratitude to Smith College and the National Science Foundation for contributing assistance, facilities, and finances towards the completion of this work. Congratulations are due the Ronald Press for its part in this fine enterprise, for the volume is pleasing in all aspects. High praise is due the committee of the Genetics Society of America which catalyzed the reaction which resulted in the publication of this labor of love.

Attention should be called to page three of the volume, which carries an invitation to investigators interested in securing material of the Jimson weed in order to add further chapters to our knowledge of the members of this fascinating genus.—ALTON H. GUSTAFSON, Department of Biology, Bowdoin College, Brunswick, Maine.

Vascular Plants of the Pacific Northwest. By C. LEO HITCHCOCK, ARTHUR CRONQUIST, MARION OWNBEY, and J. W. THOMPSON. Illustrated. University of Washington Press. Part 5, pp. 1–343. 1955. $7.50. Part 4, pp. 1–510. 1959. $12.00.

Present or future students of the Pacific Northwest flora will find their time well spent in carefully looking through the two volumes now available of the projected five-volume "Vascular Plants of the Pacific Northwest." It is a credit to the authors that they have drawn on their wide experience in the western flora to point out and discuss specific problems such as unusual variation patterns, possible hybridization, disjunct or vicarious distributions, and a host of other phenomena which suggest a number of areas requiring the attention of biosytematists, plant geographers, genecologists, and cytologists. This is merely a bonus added to a sound taxonomic treatment of the 4000 vascular plants (upon completion) either native or introduced in "all of Washington, the northern half of Oregon, Idaho north of the Snake River Plains, the mountainous portion of Montana, and an indefinite southern fringe of British Columbia." The area circumscribed is a natural floristic unit and excludes most of the interesting but large Great Basin flora occurring in the southern portions of Idaho and Oregon as well as the sizable cluster of endemic or California-centered species characteristic of southwestern Oregon.

The two volumes published to date are Parts 4 and 5 of the series: Part 5 is a monograph of the Compositae by Arthur Cronquist and Part 4 includes treatments by Cronquist (Polemoniaceae through Campanulaceae, except *Castilleja*), C. Leo Hitchcock (Ericaceae through Cuscutaceae), and Marion Ownbey (*Castilleja*). Although J. W. Thompson has not yet contributed texts, his valuable and extensive collections in the Northwest serve as a substantial basis for the present knowledge of the northwestern flora, hence his inclusion as a co-author is fully justified even in the absence of such textual material. The families are arranged in the Englerian sequence; the genera and species within a genus are arranged alphabetically. This practice eliminates the need for an index, although one to the synonyms of the larger genera and to common names is included. The chief difficulty with this alphabetical arrangement is that closely related species and genera are placed together only rarely, thus rendering a character-by-character comparison of two taxa (as is often done during the course of identification) rather more difficult. Taxonomic concepts are admittedly conservative, which results in the volumes being attractive for purposes of identifying species of such name-ridden genera as *Aster, Castilleja, Erigeron,* and *Senecio*.

In Part 5, Cronquist outlines his philosophy of taxonomy, which we assume to be the philosophy of the other authors as well in the absence of any statements to the contrary. His discussion is worth reading since he presents particularly well his views as an "orthodox" taxonomist on some of the attitudes held in the past by experimentally oriented workers. The term *variety* is preferred to *subspecies* when only one infraspecific level is recognized. In a few instances where it has been necessary to utilize two infraspecific levels, *variety* is subordinate to *subspecies*; *forma* is not used. It is a reflection of the authors' conservatism that infraspecific categories are widely used for entities which other workers prefer to recognize as species. In attempting to conform to their system, numerous changes in rank of many taxa have been made, involving transfers from subspecies to variety. Fortunately, these changes have been rendered somewhat inconspicuous by their placement among the synonymy of the species. The synonymy of each species is laudably complete and gives the full bibliographical citation, the collector, locality, and date of collection for the type of each synonym.

The volumes issued to date have served as vehicles for the publication of three highly localized species: *Chaenactis thompsonii, Hackelia davisii,* and *Luina serpentina*—appropriately endemic to Washington, Idaho, and Oregon respectively. In addition to these new species, numerous varieties are described for species of many genera. This emphasizes the fact that the Pacific Northwest is far from completely known botanically. In addition to these novelties, numerous changes of rank and transfers from one taxon to another are made. Hence this work can hardly be called an automatic compilation; rather it is an original, critical treatment of all the species it covers. The geographical ranges of the taxa are specifically outlined and, where known, ecological data regarding the habitat are included as well.

Although the authors have made extensive use of existing taxonomic monographs (many of which are cited in the text), they have obviously felt no obligation to follow these works in their own treatments. Undoubtedly they will receive criticism for their handling of many groups, but the citation of monographs and the lists of synonyms will make it easy for those who do disagree on some count to find other interpretations of the group in question. The Menyanthaceae and Gentianaceae are considered separate families; on the other hand, the Lobeliaceae are included in the Campanulaceae. Genera of the Vacciniaceae, Pyrolaceae, and Monotropaceae are found within the Ericaceae. *Ipomopsis* is relegated to *Gilia* and *Cacaliopsis nardosmia* will be found as a *Luina*.

The work serves as an interesting chronicle of the fate of many weedy introductions into the area. For instance, we learn that *Anthemis mixta* L. and *A. altissima* L. have both been collected only on the famous ballast heaps at Portland and presumably have failed to become members of the naturalized flora of the Pacific Northwest. This is quite different behavior from that of their cogeners *Anthemis* *cotula* L. and *A. arvensis* L., which have been extremely successful in becoming established in the region as weeds. *Conyza floribunda* H.B.K. and *Tournefortia sibirica* L. have apparently only persisted at their point of introduction and are not expanding in range. But by far the largest number of weeds have become widely distributed in the region and most, if not all of these are discussed in the text. These different patterns of behavior subsequent to introduction suggest a fertile field for genecological studies.

Notes on the cultivation and ornamental value of many of the native species included in Part 4 have been supplied by two accomplished Seattle horticulturalists: Carl English and Brian O. Mulligan. These men and a number of other northwestern gardeners have demonstrated the high desirability of native plants in the garden when they are grown properly. The ornamental value of the northwestern flora is not as widely appreciated in this country as it deserves to be; it is probably easier to purchase seeds of Northwest Pacific Coast indigens from British and European nurserymen than from American ones. It is true that attractive species such as *Gaultheria shallon, Arctostaphylos uva-ursi,* and *Arbutus menziesii* are rather widely grown, yet too few gardeners are aware of the potentialities of equally attractive species such as *Menziesia ferruginea, Vaccinium ovatum* and *V. parvifolium,* and *Polemonium carneum.* The majority of these species can be propagated or obtained in a manner which does not involve denudation of the countryside. Understandably, horticultural notes have not been included for the Compositae, whose contribution from the temperate zone of a large and diverse assemblage of weeds largely outweighs its contribution of a depauperate ornamental flora.

Chromosome numbers are included for most of the taxa in which they are known, although the literature sources for these numbers are not given. In the instances of circumboreal or polytypic species, or of polyploid complexes, it would be valuable to know the geographical source of the plants on which the counts are based.

Despite the necessity of using the same type throughout the entire work, the format of the book is enlivened by consistent use of indentations, capital letters, and underlinings for various kinds of information repeatedly appearing in each species description. Part 5 appears to be free of typographical errors; there are, however, several errors in Part 4 but none has been found which seriously impairs the meaning or usefulness of any section of the book. Each species discussed is illustrated; the Compositae were drawn by Dr. John Rumely and the taxa in Part 4 were done by Jeanne R. Janish, who is well known in the west for her work on Abrams' "Illustrated Flora of the Pacific States." Both artists have provided a felicitous combination of accurate scientific illustration with esthetically pleasing artistry. Dr. Rumely's drawings lack some of the three-dimensional qualities of Mrs. Janish's and are more obviously based on herbarium specimens; this may, however, prove to be something of a virtue in view of the high likelihood that most botanists would prefer to bring their specimens back from the field in press, rather than carry these bulky volumes with them in the field.

The keys are quite usable and generally include a number of characters which can be utilized in identifying an unknown species. Since the series is not yet complete, no glossary of terms or key to the families is provided. However, the publishers promise a family key in Part 1, and the authors promise that "a more nearly natural arrangement of the families and orders of dicotyledons will be presented at the beginning of Part 2." The high caliber of the work that has so far appeared makes us eagerly await the completion of this valuable contribution to the knowledge of the flora of the Pacific Northwest.—Robert Ornduff, Department of Botany, University of California, Berkeley.

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